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The taxonomy, mode of life and ecology of the callovian crocodiles from the East Midlands of England.

Tresman, S M Adams

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THE TAXONOMY, MODE OF LIFE AND ECOLOGY OF THE CALLOVIAN CROCODILES FROM THE EAST MIDLANDS OF ENGLAND

VOLUME ONE

by

SUSAN MARY ADAMS-TRESMAN

Department of Zoology

Kings College - University of London

Department of Palaeontology

British Museum (Natural History)

Thesis submitted for the degree of Doctor of Philosophy in the University of London.

October 1980

ABSTRACT

THE TAXONOMY, MODE OF LIFE AND ECOLOGY OF THE CALLOVIAN CROCODILES FROM THE EAST MIDLANDS OF ENGLAND

by

SUSAN M. ADAMS-TRESMAN

For many years the taxonomy of the Callovian marine crocodiles contained in the Leeds Collection has been in a state of confusion.

Bivariate and principal coordinate analyses have been used here to attempt to identify discriminatory cranial characters which could be used to classify species belonging to Steneosaurus, Mycterosuchus and Metriorhynchus.

Many of the characters previously used to define seven Callovian species of Metriorhynchus and five of Steneosaurus and one of Mycterosuchus are individually, or continuously variable.

A revision of the currently accepted taxonomy is consequently proposed:

A single species S. leedsi will include all Callovian species of Steneosaurus in addition to those presently included in the genus Mycterosuchus.

Two species for the genus Metriorhynchus are proposed which can be distinguished on the basis of their skull proportions: M. superciliosus and M. brachyrhynchus.

The existing osteological descriptions of these genera are re-examined, and the data synthesised with new evidence presented largely as a result of neontological - palaeontological comparisons. This information shows that the disparity between the niches the crocodiles inhabited: (i.e. steneosaurs in coastal or beach provinces; metriorhynchids in open marine) which was based on their contrasted morphologies, has been exaggerated previously as a result of cursory examination of available Callovian material. Examination of the osteology of the steneosaurs suggests that their anatomy would not preclude them from sharing similar environments with the metriorhynchids.

A palynological investigation into the "crocodile bearing" sediments produced information of ecological and environmental significance, which was synthesised with Duff's (1975) Callovian biostratigraphy for the East Midlands.

These data indicate the strong influence of the London Platform over the shelf sea environment which the crocodiles inhabited, and on the basis of new information presented here, a revision of the form of the London Platform coastline is suggested. This environment is contrasted with the coastal or beach province apparently inhabited by Bathonian steneosaurs from the Oxfordshire region.

Palynological results from jason Zone lithologies from the field are compared with those obtained from matrix attached to steneosaurs and metriorhynchids contained in museum collections.

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THE TAXONOMY OF THE CALLOVIAN MARINE CROCODILES

INTRODUCTION

"The Leeds Collection is unique and likely to remain so" (E. T. Leeds 1956). The importance of this collection of fossil reptiles, fish and some invertebrates, stems from the circumstances and opportunities which existed throughout thirty years of collecting by the Leeds family, in brick works and quarries. At this time, methods of clay excavation facilitated large scale collecting, the clay being worked by manpower (see Plate 1) and innumerable fossil vertebrates and invertebrates were extracted with it.

Without the skilled collecting and appreciation of Charles, and later Alfred N. Leeds and his son E. T. Leeds at the close of the last century when the clay pits of Peterborough were in full production, this wealth of palaeontological material would probably have been partially lost, or its value diminished by dissociation of specimens in local museums. The advance in commercial efficiency, and coincident methods of clay quarrying within the brick manufacturing industry, has resulted in a vast reduction in opportunities for excavating fossil remains from these quarries, and thus the possibility of assembling or augmenting such a superb collection is now extremely remote.

A brief history of the events that led to the formation of the collection can be found in "The Leeds Collection of Fossil Reptiles from The Oxford Clay of Peterborough" (E. T. Leeds, ed. Swinton 1956), and in addition, fascinating detail of sites of discovery of components of the collection, dates and methods of collection and details of their stratigraphic distribution (albeit indirectly)!

"In the latter pit, the clay belongs to a higher zone than that of the Fletton group (of pits), or even that of Dogsthorpe, since it is largely situated north of the great Essendine fault, which must actually run through the Eye, north of Dogsthorpe pits. As a result, the Eye pit, though

richly productive of pyritised ammonites, which in the lower zones were only obtainable as flattened shell impressions, was almost sterile of reptilian remains." (E. T. Leeds 1956 p. 19). We can couple this information with present knowledge of preservation of ammonites in successive zones of the Callovian to effect a crude location of vertebrate material. This work also contains detail of the physical characteristics of the material and its mode of preservation and detail of numbers of species and the anatomical elements of the various groups comprising the collection. At present the collection is mainly accommodated in the B.M. (N.H.), other specimens being housed in the Hunterian Museum of Glasgow University and the National Museum of Wales, with important supplementary material in the Oxford University and Peterborough Museums.

The Leeds Collection contains a number of marine crocodiles, which form the nucleus of the material examined in the course of this study. These crocodiles, belonging to the suborder Mesosuchia, occur in the Jason and Coronatum zones of the Oxford Clay. They were found principally in a small geographic area of Northamptonshire, close to Peterborough, though specimens are rarely found also in more southerly outcrops of Oxford Clay.

For many years the taxonomy of these crocodiles has been in a state of confusion, resulting from the scant attention paid to the group after Andrews' monumental contribution in 1913, which was augmented by later workers who applied his ideas uncritically. At present we have no detail of the exact stratigraphic position of these crocodiles, of the ecological relationships between genera and their habitats or any detailed appraisal of contemporaneous invertebrate faunas. No matrix from these crocodiles was ever made available for study in this context and, until now, no analyses attempted. This study aims to provide new insight into these areas.

The present study includes a revision of the systematics of this group, and examines some aspects of their biology, ignored by previous workers.

The information that is available consists of many mutually contradictory statements. The study has involved the application of methods by which can be synthesised the information made available by location and examination of scattered Leeds Collection and supplementary material. In addition, the material Andrews (1913) worked with has been revised, in order that the information contained therein can be presented in a form that permits direct comparison and correlation between all marine crocodilian material belonging to the Leeds Collection.

HISTORICAL REVIEW

In his "Preliminary Discourse" to Volume 1 of his "Recherches sur les ossemens fossiles de quadrupedes" Cuvier (1812) presented and synthesised his theories of sudden major changes in physical geography occuring during the Earth's history which he termed "revolutions", and used them to provide an explanation for the mass extinction of functionally well adapted animal species. Examples were contained in the volumes of the above work (1824 second edition) which consisted of revised versions of his previous monographs on the osteology of various fossil and related living species of tetrapod vertebrates. One of these volumes, number 5 (2) contained descriptions of some fossil crocodiles, with some comparative study between fossil and living species.

In 1825, Geoffroy St. Hilaire produced a rival interpretation to Cuvier's "Revolutions of Life" outlined above, implying in the title of his memoir (1825) that the living species (of crocodiles) "had descended by an uninterrupted path of generation from the fossil species" (p.97). In addition he presented the crocodiles described in 1824 by Cuvier as evidence in support of his argument that the anatomical difference seen in the fossil crocodiles as compared with living species had been induced by changes in the environment (i.e. that external influences could affect

development). This was in direct contrast to Cuvier's theories, and implied that animal organisation was more labile than allowed by Cuvier's principles and beliefs, i.e. that the functional stability of animal organisation was rigidly programmed from conception. This highlights the rather unique role occupied by the marine crocodiles in illustrating aspects of one of the earliest formalised debates on the above aspects of evolution.

St. Hilaire established the generic name Steneosaurus in this memoir (1825) for the crocodilian remains known by Cuvier as the Gavials d'Honfleur in 1824. He proposed two species S. rostro major and S. rostro minor, the former relating to Cuvier's "gavial a museau plus allonge", and the latter, his "gavial a museau plus court", although neither of the above species was satisfactorily defined. This situation was further complicated, with respect to Cuviers "gavial a museau plus allonge" due to the authors reconstruction (i.e. Cuvier's) of the aforementioned specimen, which was in fact a composite specimen, comprising the snout of a steneosaur joined to the skull of a metriorhynchid. According to E. E. Deslongchamps (1866), it was Geoffroy St. Hilaire who subsequently renamed S. rostro major, calling it S. megistorhynchus.

In 1825 von Meyer created a new genus Metriorhynchus to describe the second of Cuvier's species above (i.e. gavial a museau plus court, 1824, 5 (2), pl. 10 figs. 5 - 7) although no species name was proposed. In 1832 M. geoffroyi was established by von Meyer for the reception of Geoffroy's S. rostro minor, based on Cuvier's "gavial a museau plus court", and this is, therefore, the type species of the genus Metriorhynchus.

E. E. Deslongchamps (1863-1869) gave the first detailed descriptions and figures of Steneosaurus and Metriorhynchus (emending von Meyer's and Geoffroy St. Hilaire's earlier descriptions of these genera) creating many new species for the material collected around Caen and Normandy and emending some earlier species, producing the first detailed descriptions

of these specimens also. (Descriptions and figures of the above begin on p. 201 in Notes Paléontologiques). In this work he established the type specimen of Steneosaurus as that specimen figured by Cuvier (1824, 5 (2), pl. 8) and named S. megistorhynchus by Geoffroy St. Hilaire (1825) while simultaneously emending the diagnosis of this species. (1869 p. 217 pl. xv).

Specimens identified as belonging to some of the species he created were subsequently found in English Jurassic sediments e.g. S. larteti (Fullers Earth of England and Calcaire de Caen) S. boutilieri (Great Oolite of England and Calcaire de Caen) S. edwardsi and S. roissyi found in the Oxfordiennes des Vaches Noires (the latter also in the Callovian of Calvados) are particularly relevant in a consideration of the taxonomy of Callovian fauna. S. roissyi was based on a mandibular fragment, probably referable to the genus Metriorhynchus Andrews (1909). Bigot (1896 a) ascribed to this species a jaw from the Callovian of Calvados which Andrews considered attributable to S. leedsi (Steel 1973).

Comparisons between S. hulkei and S. durobrivensis and S. edwardsi are particularly important in the revision of the taxonomy of this genus. Unfortunately a large amount of the type material described by E. E. Deslongchamps was destroyed or misplaced during the last war, and so vast amounts of vital information have been lost for ever and one must rely in the case of the above species entirely on E. E. Deslongchamps' descriptions and text-figs. to effect the comparisons.

Three of the species belonging to the genus Metriorhynchus described by E. E. Deslongchamps (op. cit.) are directly relevant to the Crocodilia found in the English Oxford Clay and contained in the Leeds Collection. M. superciliosum, M. moreli and M. brachyrhynchus are found in sediments ranging in age from Am. lamberti to Am. cordatus in the Oxfordiennes of Vache Noires. The type material for the latter two species disappeared during the war, and their validity must be discussed on the strength of

E. E. Deslongchamps' representations.

Lydekker, (1890) described and figured the symphysis of a mandible presented to him by A. N. Leeds, concluding, from his detailed descriptions, that it belonged to a crocodilian genus and species unrecorded from the Oxford Clay. He compared the specimen with E. E. Deslongchamps' descriptions and figures of the genera Steneosaurus and Metriorhynchus, and listed those distinguishing features of the specimen from the former genera. In his diagnosis, emphasis was placed on the number, relative size and arrangement of the most anterior teeth, comparisons being effected with E. E. Deslongchamps' reconstructions. He noted some details of another imperfect skull in the Leeds Collection which he (and Leeds), believed also to belong to Metriorhynchus. By comparison with Deslongchamps' figures, the skull was seen to share many of the features characteristic of this genus, although differing in a broader rostrum, shorter nasals, fewer teeth which differ in density of striae and degree of compression from those of other species belonging to this genus. Lydekker believed the skull and figured mandible belonged to the same species and that this material proved the existence of a crocodile "allied in cranial characters to the metriorhynchids..... but distinct from all named forms with which I am acquainted". (p. 288). The distinguishing characters were said by him to be sufficiently important to be regarded as of generic value, therefore he named the specimen Suchodus durobrivensis.

Lydekker's work predates that of Andrews and the collection of large quantities of crocodilian material by the Leeds family. If he could have seen this material, it would undoubtedly have influenced his conclusions, particularly his appreciation of the range of individual variation which he instead attributed to generic differences. His conclusions are very interesting, reflecting the influence of E. E. Deslongchamps' work on the formation of new genera and species at this time, and limitations imposed by the amount of excavated material.

Referring to the work of E. E. Deslongchamps, Fraas (1902) distinguished three groups of species within the metriorhynchids, characterised as follows:

1. Forms with a short muzzle, nasals in contact with the premaxillae, very large prefrontals, strong teeth: M. brachyrhynchus.

2. Forms with a strong squat muzzle, nasals separated by a considerable gap from the premaxillae, rather large prefrontals, very tough set of teeth, with less than 25 teeth in the upper jaw: M. hastifer (Kimmeridgian).

3. Forms with an elongated muzzle, narrow but strong, nasals despite their length, widely separated from the premaxillae, relatively small and far from prominent prefrontals, teeth more than 25, protruding and relatively weak: M. superciliosum, M. moreli and M. blainvillei. (According to Wenz (1968) synonymy between the latter species and M. superciliosum appears likely, although the destruction of the only specimen of M. blainvillei during the last war makes it impossible to verify this).

In his classification therefore, Fraas places particular emphasis on the length of the rostrum, form of prefrontals, number of teeth and separation of nasal and premaxillae.

In this work Fraas also created the sub-order Thalattosuchia for the most highly adapted of the marine crocodilians he worked on, with one family Metriorhynchidae (Fitzinger 1843). In this context, many of his conclusions were based on detailed descriptions of the genera Dacosaurus and Geosaurus (Kimmeridgian).

In 1904 Schmidt created the species M. jaekeli for a specimen from the Oxford Clay, which has subsequently been shown to be a synonym of M. superciliosum.

Andrews (1909) described "Some new Steneosaurs from the Oxford Clay near Peterborough" and it is here that the type descriptions of S. leedsi, S. durobrivensis, S. obtusidens and S. nasutus can be found. Reference is made to the author's forthcoming catalogue which will contain more

detailed descriptions of these, and more vertebrate skeletons. This catalogue was published in 1913 and was a major contribution to the available information being of a descriptive nature and including work on steneosaurs and metriorhynchids. This section was based on the Leeds Collection Crocodilia, housed in the B.M. (N.H.). In this work Andrews erected a new genus Mycterosuchus to accommodate the specimen he originally described (in 1909) as a species of Steneosaurus i.e. S. nasutus, but subsequently considered to merit generic separation. He simultaneously revised and expanded the remainder of his descriptions of the steneosaurs. In this catalogue he distinguished the following four species from the Peterborough area:

1. S. leedsi - said by Andrews to be especially characterised by the great length and slenderness of the rostral portion of the skull, preorbital length stated as 73% of the whole, symphysial portion of the mandible 58% of total length. Characterised by the great distance and separation of nasals and premaxillae, and number and form of teeth.

2. S. hulkei - snout comparatively short, stated as under 60% of total skull length, nasals separated from premaxillae by a shorter interval than in S. durobrivensis (see below). Anterior angle of the frontal is blunt and far behind the anterior angle of the prefrontals. Symphysis of the mandible 40% of total length. Teeth relatively large. Neural spines of dorsal vertebrae lower than on S. durobrivensis, scutes different, having shallower and widely separated pits, elongated in a transverse direction.

3. S. durobrivensis - rostrum of moderate length, preorbital region 61% of the whole, orbits smaller than S. leedsi, temporal fenestrae very large. Symphysial region of the mandible occupies about 44% of its length. The frontals terminate anteriorly in a very obtuse angle, a little way in front of the level of the anterior rim of the orbits. Again, number and form of teeth are quoted. Scutes with large and

shallow pits, which do not show any tendency to elongation or a linnear arrangement, as in S. hulkei.

4. S. obtusidens - this species is distinguished by Andrews, mainly by the form of the teeth, which are blunt and rounded at the tips. He notes, however, "that some of the replacing teeth in the type skull of S. durobrivensis are somewhat similar in form..... and although other differences between that species and the present one exist, the possibility that the specimens upon which the latter is based may be very large and old individuals of S. durobrivensis cannot be ignored" (pp. 130/131). The percentage of the rostral portion of the skull is stated as 52%, the symphysial region of the jaw as 42%. Tooth number is mentioned, as is the relationship between the frontal and prefrontal bones.

Andrews erected three new species of metriorhynchids for individuals collected from the Peterborough district, which he distinguished from species erected by E. E. Deslongchamps, Lydekker etc. His 1913 catalogue contains very detailed and lengthy descriptions of the characters by which these species may be recognised, and are distinguished from other species belonging to the genus. In doing so he accepts E. E. Deslongchamps' taxonomic criteria uncritically and reiterates part of it, classifying the metriorhynchids firstly in terms of ornament of the cranial bones and proportions of the skull, and secondly using qualitative information to subdivide these initial groups.

(a) Forms in which the surface of the cranial bones is without sculpture.

1. M. laeve - A small species with a narrow skull, teeth numerous and close set, upwards of thirty on each side of the mandible. (Text. fig. 73A).

2. M. leedsi - Skull broader and more massive than in 1. Teeth large and close set, about thirty six in each maxillae. (Text. fig. 73B).

(b) Forms in which the surface of the cranial bones is more or less

sculptured with pits and grooves.

i) Narrow skulled forms:

3. M. superciliosum - A narrow skulled form in which the surface of the frontal is sculptured with sharply defined pits. The frontal extends forwards nearly to the level of the anterior angle of the prefrontals and its length in front of the orbits of the temporal fossae is considerably greater than the least width between the orbits. About twenty five teeth in each maxilla. (Text. fig. 73C).

4. M. moreli - A narrow skulled form in which the frontal bears a sculpture of shallow and, as it were, partly obliterated pits, its anterior angle does not extend forwards to the level of the anterior angle of the prefrontals and its length in front of the temporal fossae is about equal to the least width between the orbits. About twenty six teeth in each maxilla. (Text. fig. 73D).

ii) Broad skulled forms:

5. M. cultridens - Skull with comparatively short rostrum in which the nasals are separated from the premaxillae by a distance about equal to a quarter of their own length. Supraorbital notch an open continuous curve, teeth smooth and with strongly compressed crowns, about twenty teeth in the maxilla. (Text. fig. 73E).

6. M. brachyrhynchus - Skull with short rostrum in which the nasals meet or nearly meet the premaxillae. The supraorbital notch forms a sharp angle, and a line joining the outer angles of the prefrontals passes behind the posterior angle of the nasals. About eighteen teeth in each maxilla. (Text. fig. 73F).

7. M. durobrivense - Skull broad with a short rostrum in which the nasals do not quite reach the premaxillae. A line joining the outer angles of the prefrontals passes through the hinder end of the nasals. About thirteen teeth in each maxilla. (Text. fig. 73G).

Phizackerley (1951) included in his paper a description and diagnosis of a new species Steneosaurus depressus, and references are made between this specimen and others in the Leeds Collection described by Andrews (1913). The extent of the examination of contemporaneous material is unknown. The type of characters used in his diagnosis include the delicate construction of the skull, rostrum 64% of the whole length, small orbits, narrow alveolar region, symphysial region 48% of total length of the mandible. His conclusions, namely "that the slender nature of skull and rostrum and shape and number of teeth are particularly distinctive of S. depressus" (p. 1191) indicate that his examination of Leeds material was superficial.

This work also includes brief descriptions and geological and stratigraphic distributions of the Bathonian steneosaurs, S. megistorhynchus, S. boutilieri and S. meretrix (see pls.19-21). The Bathonian specimens are of particular relevance to later sections of the work. The validity of the species S. depressus will also be discussed.

Kälin (1955) reviewed the range in cranial and post cranial morphology exhibited by recent crocodilians and also the extent of morphological variation which results from growth. In conjunction with Mook's work (1921a) this provides a basis or rationale for the interpretation of osteological variations seen in fossil crocodilians, which have a fundamental bearing on their taxonomy. He included a reappraisal of the relationship between the terminology used by previous authors in respect of prosuchians, mesosuchians and eusuchians (see Kälin 1955 p. 713) which is very valuable, and also an investigation into the phylogenetic relationships between members of these sub orders. This is effected by assigning primitive or progressive character states to morphological characters, or character combinations, which are present to varying degrees in the various families. (see loc. cit. pp. 714 and 715 and table II, 716 and 717). The resultant phylogenetic relationships, based on the above, are displayed in his table III p. 719.

The work includes a systematic section in which genera and species belonging to all families of the three sub orders listed above are recorded and are accompanied by figures and descriptions of diagnostic cranial features. In addition he gives details of limb and girdle osteology, in particular diagrams illustrating the progressive modification between Protosuchus, Steneosaurus, and Metriorhynchus and Alligator limb girdles. This is the first synthesis of these relationships and contrasts the previous meticulous, but isolated descriptions of skeletal elements (e.g. Andrews 1913).

Wenz (1968) places her work in a historical perspective, with particular reference to the works of E. E. Deslongchamps (1868), Lydekker (1890), Schmidt (1904), Leeds (1908) and Andrews (1913). Her study is based on a new specimen discovered from the Peltoceras athleta zone of the French Callovian of Villers-sur-mer, the type specimen of M. superciliosum, and a selection of metriorhynchid skulls in private collections and the Paris Museum, comparisons being drawn with a single skull from the Peterborough Oxford Clay. Matrix attached to these skulls indicates a Callovian age.

Wenz establishes two groups for the metriorhynchids, with reference to Fraas' and Andrews' divisions of this genus (see pp. 23, 25 and 26) but gives an indication of the difficulties involved in establishing species within these groups. She gives a brief critique of the type of characters that have been used in species determination until now, in the light of a consideration of age and individual sources of variation in crocodilians, referring to Kälin's observations on age variations (see p. 27). She endorses the synonomy between M. superciliosum and M. jaekeli, suggested in 1907 by Leeds and again in 1913 by Andrews and suggests synonomy between M. blainvillei and M. superciliosum, although the verification of this is made impossible through destruction of the specimen in the last war. She notes that the type specimen of M. moreli was destroyed in the war and, therefore, that the appearance of this species

can only be discussed on the strength of E. E. Deslongchamps' figures. Study of individual variations (and age) in living crocodilians leads her to doubt the value of certain taxanomic criteria established by previous authors. Her work is based on the analysis of a limited sample from the genus Metriorhynchus for which she considers a limited range of characters and she recognises the need for a detailed examination of English Oxford Clay specimens before a comprehensive resolution of the taxonomy can be effected. She does not, therefore, present any formal revisions of the present taxonomy of the metriorhynchids. She rejects the Sub-order Thalattosuchia erected in 1902 by Fraas (of which the Metriorhynchidae is a family), as it is based on the extent to which marine adaptations have developed, whereas protosuchians, mesosuchians and eusuchians correspond to stages of evolutionary organisations. Wenz thereby agrees with Kälin's (1955) conclusions.

An additional important result of this work has been the recording and description of some of the specimens collected since the destruction of much of E. E. Deslongchamps' type material in the war and the statement of the stratigraphic levels and geographic localities of metriorhynchid specimens in France.

In 1970 Wenz produced a descriptive paper entitled "Sur un Metriorhynchus a museau court", including in this work some more thoughts on the taxonomy of the species M. cultridens, M. durobrivense, M. brachyrhynchus, being in favour of provisionally retaining the above three species. She concedes that with the limited material to which she has access, the situation is problematical and controversial. Wenz relates the species described in this paper to M. durobrivense, but mentions how similar the specific features are to M. brachyrhynchus and M. cultridens.

de Gasparini (1972) included in a basically descriptive paper an argument for the retention of Fraas' Thalattosuchia, as an Infra-order of the Sub-order Mesosuchia. In her opinion the Sub-order is designated

on the attainment of a combination of certain characters, which display evolutionary relationships, whereas the Infra-order is based on a grade of adaptation to a marine habitat which, she believes, justifies a separation taxonomically from the Mesosuchia at the level of Infra-order.

In 1974 Mateer included in his paper descriptions of two specimens of M. superciliosum from the Oxford Clay of Peterborough, which are in the collection of the Uppsala Museum. Mateer's descriptions are restricted to the "diagnostic features as far as possible" (p. 54), which are taken from Andrews (1913), and he refers the reader to this work for "general anatomical details of the species" (p. 54). It is apparent that Mateer accepts the definitions and diagnoses given by Andrews uncritically, without questioning the validity or significance of characters used in these diagnoses.

In 1977 de Gasparini & Diaz made an important contribution to the literature with their discovery and description of a well preserved Metriorhynchus skull for which they created the species M. casamiquelai from the Callovian of northern Chile. In their description, they refer to the work of E. E. Deslongchamps (1869), Fraas (1902), and Wenz (1968). E. E. Deslongchamps (1863-69) recognised the "the genus Metriorhynchus is easy to define but not the characterisation of its species". (p. 292). de Gasparini & Diaz mention the various anatomical elements which have been given systematic importance by previous workers. Most relevant to their introduction of the new species is Wenz' (1968) conclusions regarding the taxonomy of the metriorhynchids, that they should be arranged into the following groups:

a) narrow, long snout, M. superciliosum, M. leedsi, M. laeve - in the retention of these separate species ornament is important.

b) big skull, short rostrum, M. cultridens, M. durobrivense, M. brachyrhynchus. They include M. casamiquelai among the second and list the following characters by which it may be differentiated from all other species in group b).

1) the prefrontal is less expanded than in M. hastifer (Kimmeridgian).

2) the frontal penetrates up to the anterior edge of the prefrontals and the frontal nasal suture is slightly rounded (in M. cultridens and M. brachyrhynchus the frontal is shorter and the suture straight).

3) the separation between the nasals and premaxillae is greater than in M. cultridens, M. durobrivense and much greater than in M. brachyrhynchus, where it reaches the greatest degree of approximation.

4) the teeth have cylindrical crowns, while grooves or carina are not seen (in M. cultridens and M. brachyrhynchus the crowns are moderately compressed and may have grooves).

5) the number of teeth on the upper maxilla equals 20/21 which approximates M. cultridens, M. brachyrhynchus and M. hastifer.

6) there is no ornamentation (all species in group (b) sensu Wenz 1968) have different degrees of ornamentation.

7) premaxillary/maxillary suture in the shape of an M (all species of the genus have the shape of a V).

Buffetaut's paper (1977) is basically descriptive with brief notes on "the way of life of the genus" based on aspects of the morphology of specimens examined. His work on the systematics is interesting - he refers to the conclusions of de Gasparini (1972) in calling the Thalattosuchia an Infra-order of the Sub-order Mesosuchia. He also notes the correct specific name of the species M. superciliosum to be superciliosus,(superciliosum according to the emendation by Lydekker 1890) although it is the former which has become entrenched in the literature, stating "The international code of zoological nomenclature stresses that (art. 30) the names ending in "rhynchus" must be considered masculine" (p. 254).

In assigning the specimen he has described to M. superciliosus he notes "specific attribution to be difficult, owing to the large number of species with questionable characteristics which have been described by

previous authors" (p.263) including E. E. Deslongchamps and Andrews. Wenz's summary of the situation (1968 and 1970) based in the main on French material, is welcomed. So also is the additional data provided by Brunet (1969) who raises some doubts as to the synonomy of M. blainvillei, M. superciliosum and M. moreli tentatively suggested by Wenz, but concedes that some specimens show a mixture of characters considered as distinctive of the species above.

RESULTING DIAGNOSES OF FAMILIES AND GENERA INTRODUCED IN THE HISTORICAL REVIEW

Crocodiles belonging to the Sub-order Mesosuchia (Huxley 1875) variously possess most of the typical crocodilian characters, as noted by Joffe (1967) including:

1) A false palate formed by the premaxillae, maxillae and palatines.
2) A pes modified to allow movement between the tarsals.
3) Dermal armour in general well developed.
4) Cranial table.
5) A pubis totally excluded from the acetabulum.
6) Amphicoelous vertebrae.

Those mesosuchians included in this study have been placed in two families. Firstly the Teleosauridae (Cope 1871), to which the genera Steneosaurus (St.Hilaire 1825 emend. E. E. Deslongchamps 1867) and Mycterosuchus (Andrews 1913) belong. The characters by which this family is defined (Andrews 1913) are as follows, elongate rostrum, formed mainly by the maxillae, the premaxillae being small and separated by a long interval from the nasals, numerous teeth. Post orbital bar superficial, supratemporal fenestrae large and containing the frontal within their margins. Prefrontals small and do not form an overhanging roof to the oval, dorsally placed orbits. Mandibular symphysis contains splenial inclusion. Armour well developed, dorsally two rows, with overlapping

plates with a peg and socket articulation, numerous ventral scutes. Forelimbs much smaller than hind, antorbital fenestrae sometimes present.

The second family, the Metriorhynchidae (Fitzinger 1843) (corresponds to Geosauridae Andrews 1913) has sometimes been placed in a separate sub-order Thalattosuchia (Fraas 1902) and contains the genus Metriorhynchus (von Meyer 1825 emend. E. E. Deslongchamps 1867). Andrews (1913) defined the family as follows:

mesosuchian exhibiting advanced aquatic specialisations. Snout of varying length and slenderness, but not sharply demarcated from the cranial table, nasals large with a considerable share in rostrum formation, maxillae may exclude them from the premaxillae. Prefrontals very large, overhang the orbits which are laterally placed, often sculptured. No terminal premaxillary expansion. Well developed sclerotic plates. Supratemporal fenestrae large, frontal entering its margins. Splenial enters mandibular symphysis. Forelimb very reduced, "paddle-like", reversed heterocercal tail, hind limb large, no dermal armour.

It is appropriate at this point to review the characteristics of the three genera contained in the collection which belong to these two families, (the validity of which will be examined in this chapter).

Andrews (1913) not only defined the genus Mycterosuchus, but also placed new species within the genera Metriorhynchus and Steneosaurus and in doing so, accepted the earlier authors suggestions of the taxonomically important characters of these genera as follows:

Steneosaurus: Snout of varying length, premaxillary region expanded and bearing united anterior narial openings, dorso-laterally placed circular orbits. Frontal small, lacking sculpture, skull table flattened, supra temporal fenestrae very large and elongate. Alveolar borders straight, palatal vacuities large. Internal nares rounded. Teeth numerous, forelimbs reduced in respect of hind, but not greatly so. Vertebrae slightly concave, tail not heterocercal, caudal vertebrae numbering

approximately forty. Dorsal armour consisting of a double row of keeled plates which are united by an overlapping peg and socket articulation numerous ventral plates.

Mycterosuchus: Snout greatly elongated and sharply marked off from the cranial region of the skull which narrows very rapidly in front of the orbits. Alveolar borders straight, slender teeth. Supratemporal fenestrae relatively shorter than in the "typical Steneosaur". Rugose sculpture of the frontal. Long mandibular symphysis, forelimb less reduced than in Steneosaurus. Long tail and dermal armour well developed.

Metriorhynchus: Skull gradually tapering, snout relatively long without distal premaxillary expansion. Large external nares, sculpture variously developed on cranial bones. Teeth lacking serrate margins, number depending on length of snout. Two sacral vertebrae and at least thirty five caudals. Forelimbs highly specialised as swimming organs, shortened epipodals in particular, flattened carpals. Hind limbs elongate.

Numerous species of Steneosaurus and Metriorhynchus have been described from sediments ranging in age from Lias to Portlandian, (for an account of these forms, see Steel 1973). This work deals primarily with specimens of Callovian age, (and some Bathonian Steneosaurs in an environmental context). The currently accepted species occuring in Callovian sediments, belonging to the genus Metriorhynchus are:

M.superciliosum (de Blainville 1853), M. moreli (E. E. Deslongchamps 1867), M.durobrivense (Lydekker sp. 1890), M. brachyrhynchus (E. E. Deslongchamps 1867), M. laeve (Andrews 1913), M. leedsi (Andrews 1913), M. cultridens (Andrews 1913).

and for the genus Steneosaurus:

S. leedsi, S. durobrivensis, S. obtusidens (Andrews 1909) and S. hulkei (Andrews 1913).

In addition to those steneosaurs listed above, Phizackerley (1951) created a new species S. depressus for a single specimen from the jason

zone, Oxford Clay. This specimen, the type, is housed in the Oxford University Museum.

For the genus Mycterosuchus:

M. nasutus (Andrews 1913).

THE SYNONOMY OF CALLOVIAN STENEOSAURS

S. leedsi (Andrews 1909, p. 300, pl. 8 fig. 1)

S. roissyi (E. E. Deslongchamps 1869, p. 23, pl. ii fig. 1)

S. teleosauroides (Auer 1909, p. 266)

S. durobrivensis (Andrews 1909, p. 304, pl. 8 fig. 2)

S. larteti var. koeni (Auer 1909, p. 224)

THE SYNONOMY OF CALLOVIAN METRIORHYNCHIDS

M. superciliosum (de Blainville 1853) MS Conybeare.

A cast of this skull was sent by Conybeare to de Blainville, who found it identical with specimens from the Oxford Clay (Vaches Noires Normandy), and adopted Conybeare's manuscript name for the species.

Crocodilus superciliosus (de Blainville 1853, 9, p. 114)

Teleosaurus superciliosus (E. E. Deslongchamps 1867, 2: 1, p. 149)

M. superciliosus (E. E. Deslongchamps 1867, p. 306-319) *

S. dasyceps (Seeley 1869, p. 140 no description)

M. jaekeli (Schmidt 1904, 16, p. 97, pls. 11 and 12)

* Amended spelling of superciliosum rather than supersiliosus in a letter from de Blainville to J. A. Deslongchamps in 1848: proposed by Lydekker 1890, (see also p. 31).

M. durobrivense (Lydekker sp. 1890)

Suchodus durobrivensis (Lydekker 1890, 46, p. 284)

RELEVANT INFORMATION ON LIVING CROCODILIANS

Certain information about living crocodilians has particular relevance to the interpretation and understanding of the Callovian marine crocodiles. The following aspects which have been investigated by the authors listed

below are particularly important:

Osteology

Mial (1878), Mook (1921 a) b) c)), Romer (1956), Edmund (1962), Chiasson (1962), Iordansky (1964, 1973), Langston (1973), Dodson (1975).

Myology

Haughton (1864/66, 1868), Gregory & Camp (1918), Romer (1923), Chiasson (1962), Iordansky (1964).

Physiology

Packard, Tracy & Roth (1977).

Ecology (includes general accounts of the life history of crocodilians)

Cott (1961), Modha (1967), Duson (1970), Neill (1971), Guggisberg (1972), Zug (1974), Dodson (1975), M^{c}Ilheny (1976), Singh & Bustard (1976), Webb & Messel (1978).

Mooks' publication (1921 a) stemmed from the difficulty he encountered in the determination of species in a study of Cuban Pleistocene crocodiles. This was a consequence of a wide range of variation in certain skull characters, coupled with close similarity in others. This study, (based on variously sized specimens from a number of species of recent crocodilians) is an attempt to determine the "value", in taxonomic terms, of the variations he observed. The author determined that two sources of the variation were encountered, age and individual. This is the first statement of the sources of variation responsible for the type of osteological variations which had been interpretated in fossil forms as having systematic importance by previous workers. For example, proportional relations of length and breadth of the skull, of preorbital and orbital-postorbital regions; size, shape and position of the supra temporal fenestrae; shape of snout; size and number of teeth; variation in the form of certain sutures and ornamentation of cranial bones.

Cott (1961), Neill (1971) and M^{c}Ilheny (1976) have documented changing ecological roles through life in Crocodylus niloticus, crocodiles and

alligators respectively, with respect to dietary change, and in terms of a series of niches which the reptiles occupy during their life history (interspecific niche differentiation by body size cannot occur in continuously growing reptiles). In consequence, the level of sympatry among living crocodilians is relatively low, being accompanied by obvious differences in snout structure, gross differences in size and major habitat differences (Dodson 1975). This information has a direct bearing on the relationship between taxonomic groups and the morphology of fossil forms.

Some of the facts presented in the literature listed overleaf can be used as a basis for inferences about the interrelationships between form, function, and ecology, and to give an indication of the morphological variability we might expect to occur, which has a bearing on our assessment of the taxonomic validity of characters in the Callovian crocodiles, for which direct observations on life habits are impossible.

MATERIAL EXAMINED

TYPES OF BIAS AFFECTING MATERIAL EXAMINED

1. Resulting from the very concentrated area in which the early brick pits were worked, and therefore collecting was possible.

All of the pre 1890 collection is recorded as having been excavated from an area ½ mile square. Within this area, according to Leeds, certain areas proved most productive. This seems to indicate that vertebrate remains in this region are concentrated.

Much more material was collected before 1890 than after that date. Leeds believed that this was because pits that were opened after 1890 (in response to the great boom in the brick trade at this time), were more remote and inaccessible. In some of these later pits "steam diggers" were introduced, initially for removal of top soil and boulder

clay, and subsequently at deeper levels within the clay pits. Such methods of quarrying were not conducive to large-scale collecting, so that pits where these methods were introduced would apparently yield less material because it turned up in disartulated, fragmented form (see p. 20 E. T. Leeds 1956). These factors, however, do not completely explain the "productivity gradient" in terms of amounts of vertebrate material discovered in relation to areas of clay exposed by quarrying between the Fletton pits and those en route to Yaxley (map opposite p. 16 E. T. Leeds 1956), the most southerly pits being the least productive of all.

This information indicates an apparent concentration of vertebrate material within the Peterborough area around Fletton. Consideration of fossil material recovered from pits in Bedford and Buckinghamshire are particularly relevant to the problem of deciding whether the known distribution of crocodilian material is wholly or in part attributable to collection bias.

London Brick Company pits were opened at Bletchley and Calvert, Bucks. around the turn of the century (it is not possible to be more accurate than this), and both were worked by hand for the initial part of quarrying (see plate 1.). Thus, they opened at a slightly later date than the Peterborough pits and the working period over which clay was excavated by hand was necessarily shorter. Also to be taken into consideration was the fact that the Leeds family were not concentrating their collecting efforts in these areas. The importance of this factor should be emphasised if we are attempting to assess factors contributing to the distribution of crocodiles, and possible sources of bias which might affect the known distribution. There are no records of visits to these pits by the Leeds family. Even so, during the period of manpowered clay excavation, numbers of vertebrates are known to have been uncovered (L.B.C. records unpubl. data), but never crocodiles. A third London Brick Company pit was opened at Stewartby, Beds. around this time, and it is thought that the pattern of clay excavation here followed that of the other pits, although it is

less well documented (J. Horrell L.B.C. geologist pers. comm.) A rare, but fairly well articulated metriorhynchid was found at Calvert and excavated by a party from Leicester University (Duff, Hudson, Clements et al 1975, unpubl. data.)

This evidence appears to indicate a geographic zonation of crocodilian material and suggests the presence of vertebrate faunal provinces within the Oxford Clay of the East Midlands.

2. Bias introduced during excavation (i.e. problems encountered in the collection of skeletons, even after their location).

E. T. Leeds (1956) remarked on the amount of material probably lost in various pits through uncooperative workmen (loc. cit. p. 19), and how the position of the fossil with respect to the working face of the quarry might influence recovery. His observations also highlight a further factor which might have biased the degree of articulation of any given specimen, that of the rapidity with which excavations of some of the skeletons had to be attempted, resulting from an "understanding with the brick yards" that this should not delay working of the pit. This bias might therefore have affected the apparent zonation of crocodilian material and the degree of articulation of the specimens.

The source of the Crocodilia, in terms of brick pits according to the date the material was collected, is recorded in chapter two of Leeds' account 1956. Unfortunately there are no detailed records of where the specimens were excavated within the stratigraphic sequence exposed in these pits. The ammonite zonation recognized today had not been established at the time of the Leeds collecting, but detailed stratigraphic information and in particular, diagrams of the location of specimens with respect to the suites of distinct lithologies which comprise the pit faces, would have enabled us to establish the exact stratigraphic relationships between all specimens.

Such information that exists (e.g. Arkell 1933) indicates a concentrated

stratigraphic and geographic occurence, supporting the theory that both genera in the Leeds Collection can be regarded as belonging to a single population.

TYPES OF PRESERVATION OF MATERIAL EXAMINED

Fully or partially articulated crocodilian skeletons are likely to be found at any level within the Jason zone but are relatively uncommon within the Obductum sub zone of the Coronatum zone. Because they have been found in a concentrated area and within the same lithology, post depositional and diagenetic effects during fossilisation are here presumed to be uniform. Many specimens show articulation beyond the degree recorded by Schäfer(1972), which typifies a large vertebrate that has undergone posthumous floating for varying and sometimes considerable distances. Many specimens in the collection include assorted limb bones and phalanges, series of vertebrae, in some cases articulated, and mandibles. Disarticulated bones do occur in shell beds, particularly the "basal shell bed" (sensu Duff 1975) and the thicker pyritic shell beds.

The individual bones comprising these specimens are flattened mainly dorso-ventrally, owing to the diagenetic compression and dewatering of the matrix, which produces a resultant loss or distortion of bone "contours" and three dimensionality. They may be fragmented because of diagentic compression and distortion, in conjunction with damage sustained during excavation from the clay, "the greatest damage (to the bones) was done by the constant jar of the crowbars..... on such brittle material as fossil bone". E. T. Leeds (1956 p. 21). Such preservation necessitated careful excavation and recovery of all fragmented or damaged material, and later reassemblage, to reproduce the material in the form we now see it.

All the clay matrix was washed from the bones soon after collection to expose surface detail of the various bones, which remained evident for all subsequent workers, "he (A. N. Leeds) had explored every cranny and

crevice (of a crocodile skull) to clean them thoroughly from the gritty and tenacious clay" E. T. Leeds (1956 p. 23).

This matrix was disposed of, and thus none ever made available for analysis. The intrinsic problem was the concept at the time of collection, that the matrix was seen as a problem which obscured detail of the skeletal elements, and should be removed and disposed of as quickly as possible. The sediment therefore, which is the element which provides vital information concerning the environment and habitat of these animals, was seen as being worthless.

MORPHOLOGY (CHARACTERS EXAMINED)

i) MEASUREMENT OF CHARACTERS

The different morphological characters used are defined in pp. and figs. 1 and 2, and their values are assembled in tables 1 and 2, (and appendix 1, parts I and II), pp. 207 - 237. Distances of less than 100 mm were measured with sliding callipers accurate to the nearest mm, and those greater than 100 mm. with a steel rule. Two readings were taken where possible and relevant (e.g. study of the limbs), and averaged. By such definition and measurement, information from dissociated collections of skeletons is made available in a form which facilitates direct, precise and objective correlations and comparisons. This synthesis of information was not previously available.

The results of variation studies of populations become increasingly reliable with an increase in sample size (Newell 1956), and therefore any increase in relevant information that is made available by the use of quantitative techniques (outlined above) is of great importance.

The initial stages in the synthesis of measured morphological characters involve consideration of those characters of the skull which have been taken as taxonomically significant by previous workers; this will facilitate an objective critique of the existing taxonomy.

DEFINITION OF THE CRANIAL MEASUREMENTS IN THE GENUS METRIORHYNCHUS

Length in mid dorsal line

Measured parallel to the long axis of the skull, from the most posterior point of the supratemporal crest to the most anterior tip of the premaxillary bones (occipital surface damaged in many specimens).

Length from the occipital condyle to tip of snout

Maximum length measured parellel to the long axis of the skull, from the most posterior point on the occipital condylar surface to the most anterior point of the premaxillary bones.

Length from the anterior end of the frontal to tip of snout

Maximum length measured parallel to the long axis (of the dorsal side of the rostrum) in the mid line, from the most anterior point of the frontal/nasal sutural contact to the most anterior point of the premaxillary bones.

Length from the anterior end of the frontal to the posterior end of the supratemporal crest

Maximum dorsal length, measured parallel to the long axis of the skull, from the most anterior point on the frontal/nasal suture, to the most posterior point on the supratemporal crest (parietal bone) which separates the fenestrae.

Length of the frontal anterior to the supratemporal fenestrae

Maximum length, measured parallel to the long axis of the skull, between the most anterior point on the nasal/frontal suture, and a line drawn tangentially to the anterior border of the supratemporal fenestrae (and at right angles to the long axis of the fenestrae).

Length of the nasals

Maximum antero-posterior length measured parallel to the long axis of the skull (rostrum) from the most posterior point on the nasal/frontal suture and the most anterior point on the nasal/Maxillary suture.

Distance between the nasals and the premaxillae

Maximum antero-posterior length, measured parallel to the long axis of the rostrum, between the most anterior point on the nasal-maxillary suture and the most posterior point of the premaxillary/maxillary suture.

Least width between the orbits

Minimum width measured at right angles to the long axis of the skull, between the most medial point of the left and right orbital cavities.

Width between the outer angles of the prefrontals

Maximum width measured at right angles to the long axis of the skull, between the outermost points of the left and right prefrontal bones.

Width between the outer angles of the quadrates

Maximum width measured at right angles to the long axis of the skull, between the outermost points of projection of the left and right quadrates.

Length of the mandible

Measured parallel to the long axis of the mandible, from the most posterior point of the angular bone to the most anterior point on the dentary bone.

Length of the mandibular symphysis

Measured parallel to the long axis of the mandible, from the most posterior point of the median symphysis (in the mid line) to the most anterior point of the dentaries.

DEFINITION OF THE CRANIAL MEASUREMENTS IN THE GENERA STENEOSAURUS AND MYCTEROSUCHUS

Total length of skull

Measured parellel to the long axis of the skull, in the mid dorsal line, from the most posterior point on the occipital condylar surface to the most anterior point of the premaxillary bones.

Length of supratemporal fenestrae

Maximum length parallel to the long axis of the skull between a medial point on the posterior margin of the fenestrae and a point similarly placed on the anterior border of the fenestrae.

Preorbital length

Measured parallel to the long axis of the skull, between the most anterior point of the premaxillae, and a medial point on a line drawn tangentially to the anterior rim of the orbits and at right angles to the long axis of the skull.

Width between the outer angles of the quadrates

(see corresponding measurement for Metriorhynchus p. 43 .)

Width of the supratemporal fenestrae

Width measured at right angles to the long axis of the fenestrae between their inner and outer edges, parallel to a line drawn midway along the maximum length as defined above.

Width of snout at anterior end of the nasals

Maximum width measured at right angles to the long axis of the skull, of a line drawn through the most anterior point on the nasal/maxillary suture.

Width of the skull at the anterior rim of the orbits

Maximum width measured at right angles to the long axis of the skull, between the outer edges of the rostrum along a line drawn tangentially to the anterior rims of the orbits.

Distance between the nasals and premaxillae

(see corresponding measurement for Metriorhynchus p. 42.)

Length of the mandible

(see corresponding measurement for Metriorhynchus p. 43 .)

Length of the mandibular symphysis

(see corresponding measurement for Metriorhynchus p. 43 .)

Collection and synthesis of the above data have been supplemented by qualitative observations for those types of characters which cannot be expressed quantitatively.

ii) BIVARIATE TECHNIQUES

A number of bivariate statistics were calculated from the data obtained from the morphological observations, in an attempt to examine aspects of taxonomy by bivariate analysis. These include combination of data and presentation in the form of ratio and percentage relationships. To assist in the resolution of this data, ordination can be produced by the ranking technique, according to the values of the characters.

The data listed in tables 1 and 2 can also be presented for analysis and interpretation in the form of bivariate plots, in which any two characters of the skull (as defined in pp. 42 - 44) can be considered. This technique necessarily imposes limitations through consideration of only two characters, in the attempt to isolate discriminatory character combinations. Consideration of combinations of three characters is possible, by consideration of the relationship between a pair of the above along one of the axes.

The purpose of the production of these statistics and plots is to test their compatibility with the present taxonomic interpretations. the ranked tables of bivariate statistics and accompanying plots quantify some of the subjective taxonomic criteria which abound in the literature - e.g. "build" and "massiveness" of the skull and rostrum (Andrews 1913 with reference to the steneosaurs).

iii) MULTIVARIATE TECHNIQUES

The final stage in the analysis of the data involves multivariate techniques and the use of principal coordinates analysis.

Resolution of the taxonomy of the crocodilians (animals which present varying degrees of morphological variation) is assisted by definition of the characters of the individuals under examination, and analysis of the

similarities between all the specimens in terms of combinations of those characters. Figs. 7, 8, 9 and 10 show that patterns begin to appear when three characters are considered simultaneously which are not evident when only two characters are analysed at any one time. This supports multivariate techniques as an important method of analysis for these data.

The crocodiles are represented by vectors for the purpose of principal coordinates analysis, each being expressed as a one dimensional array of numbers, all of which are necessary to define the particular crocodilian specimen.

It is possible to represent the collection of specimens (i.e. the vectors representing the crocodiles) as points in n dimensional space (n = number of crocodiles in the population-1), with distances between them given by 1-similarity (between all possible pairs).

The first principal coordinate (or first eigenvector) is that direction along which variance (in terms of points in n dimensional space) is greatest, and the direction at right angles to this, along which variance is greatest, is the second principal coordinate. All these points can be projected onto the plane defined by these two eigenvectors, with the least possible distortion. In this instancæ the eigenvectors are defined in terms of crocodile specimens and they give coordinates of the crocodiles in the first and second dimensions. In computing similarity values for all possible pairs, data for a particular character will merge with other data, and this affects the interpretation of the information. We are looking at the relative positions of specimens in terms of their similarities to each other and have to interpret what those similarities mean in terms of characters.

It is not possible to use principal components in this analysis, in which the vector for each crocodile gives it a position in n dimensional space. The number of dimensions in this case is determined by the number of characters measured and not by the number of specimens. Because some of the values are missing, however, (as is common in palaeontological

material), we do not know the exact position of each crocodile in terms of the characters defining the vectors. (It is possible to use these position vectors to find the principal axes, the eigenvectors in this instance being defined in terms of characters and interpretation is therefore much easier).

Associated with each eigenvector is an eigen value. This indicates how much of the total variation defined by characters considered in each vector is accounted for by each principal coordinate axis.

TAXONOMIC PROCEDURES

A taxonomic study of Callovian marine crocodilian specimens should begin with an appraisal of the methodology employed in the erection of the existing classification.

Both Andrews and E. E. Deslongchamps assigned typological categories to the crocodilian material they analysed. According to this concept, each species consists of a type, and of any other specimens which appear to be closely similar to that type. The result is that each species is viewed as virtually invariable.

A consequence of the acceptance and application of this concept was the disregard of the range and pattern of variability of organisms. Andrews' and E. E. Deslongchamps' reasoning in establishing or endorsing the taxonomy of the Callovian marine crocodiles might have been influenced by the ideas synthesised later by Newell (1956) as follows:

1. The appeal of the typological concept of the species lies in its simplicity, the author is not obliged to undertake systematic mathematical studies of material.

2. Methods of study employed under this concept favour small samples because specimens supplementary to the type add little to the knowledge of the species. The type specimen defines the species, although the

types are chosen arbitarily under the typological system and do not necessarily represent the most frequent condition of this character in the population.

This gives us some insight into why Andrews never viewed or analysed very many specimens. He probably thought that the extra material would have little or no scientific value in the erection of his taxonomy. Individual variants may be conspicuous in small samples because of the incompleteness of representation of the population range, and this is the present situation with respect to characters given taxonomic importance by previous workers. Larger samples show the variants to form a gradational morphological series in which certain character states are possessed by individuals in greater relative abundance, i.e. by more individuals. "The investigator.... may regard the series as a single variable species embracing many variants previously described under other names" (Newell 1956 p. 72).

Recent palaeontology tends towards application of aspects of this neontological species concept, based on studies of the structure and variation in populations. This is a fundamentally different concept of the species and, with this in mind, much revision has been commenced of fossil species that were based on small samples, with morphological standards established in the type specimen.

It appears that when analysing the morphology of the crocodiles, Andrews and E. E. Deslongchamps paid great attention and attached importance to minor differences in the spatial relationships of the snout bones, prefrontal and frontal bones and character and number of teeth for instance.

The typological concept necessitated the evaluation of minor differences between specimens in terms of systematic importance, without searching groups of individuals for shared features, and considering variation of characters in the light of basic morphological similarities.

Andrews' work is proof of his diligence, as shown in his major work "Catalogue of the marine reptiles of the Oxford Clay" (1913). His observations with respect to morphological detail of the skeleton are meticulous, his descriptions lengthy, his measurements accurate. His skill in describing the skeletons of the steneosaurs and metriorhynchids can be measured by the fact that no further attempt to add to the written descriptions of the generalised skeleton of the above genera has been attempted in the present work. I believe that no further contribution to the morphology of these crocodiles can be achieved by repetition of these descriptions. The major taxonomic problems have arisen from other aspects of his methodology (based on the typological species concept and outlined on the previous pages).

The Leeds Crocodilia were excavated from pits which were closely associated in a geographical and stratigraphical sense. Subsequent to A. N. Leeds death however, sections of his collection became geographically isolated in a number of museums dispersed throughout the British Isles. Thus, access to all parts of the collection (and relevant material from other collections), may have been a problem to Andrews. It is difficult to know whether, in fact, he did see any of these Crocodilia, but he makes no mention of them in his work and one must conclude that even if he saw any of the other material, it played no part in his conclusions (1913).

Thus Andrews bases all his analyses on material housed in the B.M.(N.H.), which amounts to the following number of specimens suitably preserved to yield valuable taxonomic information (number of specimens given in brackets):

S. leedsi (2), S. hulkei (1), S. durobrivensis (2), S. obtusidens (2), Mycterosuchus nasutus (1)

M. laeve (2), M. leedsi (2), M. moreli (4), M. superciliosum (4), M. cultridens (2), M. brachyrhynchus (2), M. durobrivense (2)

This compares with the maximum sample, analysed in the present study, as follows:

S. leedsi (5), S. hulkei (1), S. durobrivensis (6), S. obtusidens (4), M. nasutus (2)

M. laeve (4), M. leedsi (4), M. moreli (7), M. superciliosum (26), M. cultridens (2), M. brachyrhynchus (4), M. durobrivense (4), M.sp. (34)

The present taxonomic problems are compounded by the subjective terms in which Andrews defines many of the characters he considered to be taxonomically significant. This makes comparisons with other crocodilian material very difficult and must have been one of the obstacles facing workers endeavouring to correlate and assimilate information and using Andrews as a source for some of this information.

Thus, in the division of the genus Steneosaurus, Andrews uses the following criteria:

a. length of the preorbital region of the skull and its percentage of the skull as a whole.

b. degree of robustness or massiveness of the cranial features, in particular the snout.

c. form and relationship of the frontal and prefrontal bones.

d. separation of the premaxillae and nasals.

e. length of the symphysial region of the jaw.

f. tooth form and number.

g. scute form.

Those characters given taxonomic significance for the genus Metriorhynchus by Andrews (who in part endorsed those stated by E. E. Deslongchamps) are:

a. size.

b. breadth of skull.

c. degree of sculpture of the cranial bones.

d. number and type of teeth.

e. the relationship between the frontal and prefrontal bones.

f. length of the frontal anterior to the supratemporal fenestra, in relation to its width between the orbits.

g. the distance between the nasals and premaxillae.

h. length of rostrum (for his "broad skulled forms").

a, b, f, g, h, may be examined quantitatively, c, d and e qualitatively. Some of these are not in fact independant characters. The length of the frontal bone, anterior to the supratemporal fenestra and the width of this bone between the orbits, together define the development of the frontal bone - the extent of which might be expected to vary between individuals. Tooth number, separation of the premaxillae and nasals, and the breadth of the skull, are all a function of the amount of antero-posterior growth versus "width" growth, which is expressed in successive elongation of the maxillae (see characters 3, 4 and 6, Table 2), e.g. the greater separation in M. leedsi as compared to M. laeve (Table 2) where the growth in M. leedsi has been concentrated in the elongation of the maxillae. So the elongation of this bone affects all the above, since the maxillae are the main tooth bearing elements.

In this work, study of the cranial features of both genera has centred on the evaluation of the features accepted by Andrews as having taxonomic validity, see p p. 24, 25, 26, with the aim of erection of possible new criteria where the former are shown to be insignificant. The methodology that I have used throughout the analysis outlined below involves the study of variation in accordance with the neontological species concept (see p. 48). Thus variation in the cranial characters can be analysed, bearing in mind acceptable or likely levels of individual variation which might occur in a population of crocodiles of all ages and both sexes (Mook 1921 a, Cott 1961, Dodson 1975). On the other hand, the occurence of slight morphological variation between any two individuals

is not automatically considered to be taxonomically significant. It therefore does not lead to a search for any feature which may show a small amount of variation, which might then be used as a means of division between individuals which may possess many other features in common (thus dividing specimens which are markedly similar in overall appearance by moderately variable characters).

RESULTS

STENEOSAURUS and MYCTEROSUCHUS

(i) Quantitative criteria

Combinations of the values defined on pp. 42 - 44 are presented in the form of ratio and percentage relationships which have been ordered by application of the ranking technique, in table 1. The ordination illustrates the wide range of overlap of values between species, and a high level of variation within species. The data presented in this table is designed to relate to the taxonomic criterion erected by Andrews for this genus.

The presently accepted species have been combined into two groups, comprising the most morphologically similar, so that group 1 includes S. leedsi and M. nasutus and group 2, S. hulkei, S. durobrivensis, S. obtusidens and S. depressus.

Reference to table 1 shows that the variation within groups 1 and 2 is greater than that between them, with the exception of character 1. This shows a very small degree of separation, of doubtful significance, but all other characters appear gradational.

Figures 3 - 10 present the results of an attempt to elucidate the taxonomic problem, by application of bivariate and trivariate plots. None of these plots show a significant tendency to form groups suggestive of the presence of two genera or six species, with the possible exception

of:

$$\frac{W \text{ at anterior end of the nasals} / L \text{ preorbital length}}{\text{Total skull length}}$$

and:

$$\frac{W \text{ at outer angles of the quadrates} / L \text{ total skull length}}{\text{Total skull length}}$$

which attempt to quantify "massiveness of snout" and "massiveness of skull" (Andrews 1913) respectively.

As such, these plots are not compatible with the present taxonomic recognition of two genera, Mycterosuchus and Steneosaurus, the former containing only one species, the latter five. (It should be noted at this point, however, that some of the diagnostic characters employed by Andrews cannot be examined quantitatately and will be considered in a subsequent section). Thus it seems that we can detect differences in length of snout and massiveness/breadth of skull and snout between individuals known at present as S. leedsi and M. nasutus and the other Steneosaurus species collectively.

These diagnostic features were identified by a consideration of a combination of three characters (see figs. 7 - 10) which were not clearly evident in the ranked charts (table 1) and bivariate plots (figs. 3 - 6) when we were necessarily confined to analysis of combinations of only two characters.

Consideration of the results presented above seems to indicate that many of the criteria, previously considered to be of systematic importance, are invalid because of the degree of individual variation.

The final stages in the analysis are an attempt to resolve the situation using principal coordinates analysis (see p.45).

The accompanying series of graphs (figs. 11 - 16) illustrate the relationships between all specimens of the genera Steneosaurus and Mycterosuchus, plotting the values on the first two axes (see p.46).

Consideration of total length in dorsal mid line of the skulls of the individuals in fig. 11b whose spatial relationships are plotted in fig. 11a, indicates that the first axis accounts for, or represents, length/size.

The decision as to whether observable difference in shape are due to a similar morphological form at a different scale, or to a real morphological difference (i.e. the basis upon which specific limits might be defined) is problematical. Size is a factor intimately associated with ontogenetic stages in the life history. Principal coordinates, however, facilitates standardisation for the effect of size on the other measured characters. Size, defined here as total length of skull in mid dorsal line, is variable 1. This is divided into all other variables (characters) and subsequently excluded from the analysis: var. 2 - 10
var. 1

The results of this procedure are illustrated by the new pattern shown in fig. 12. If the various specimens are ranked according to length (size) so that 1 = smallest and 17 = largest, and these rank numbers are plotted on an overlay of fig. 12 (see fig. 13) no size trend is apparent, in contrast to the situation depicted in fig. 12.

Standardisation techniques show that the relationships shown in fig. 12 do not rely in the main on their overall size, but on other characters.

It is interesting to examine the morphological relationships between Bathonian and Callovian steneosaurs as illustrated in fig. 14. From a purely taxonomic viewpoint, it was thought necessary to exclude the former from the data matrix, which could then be reprocessed and subjected to identical standardisation techniques. Figs. 15 and 16 illustrate

this part of the analysis. The associations between Callovian species are not significantly affected by the exclusion of the Bathonian specimens. One interpretation of figs. 15 and 16 would be to suggest two groups of specimens which, on the basis of comparison of all measured characters simultaneously, are linked internally by similarities in excess of those which exist between members of these two groups. The measure of similarity between any two specimens is quantified by the value of the similarity coefficient for that pair. This is a numerical expression of the morphological similarity existing between all specimens analysed, in terms of the characters measured. In fig. 15 the groups are linked internally by similarity values in excess of 78%, links between members of these groups falling below this value. Examination of the value of the similarity coefficient linking the most similar end members of these two groups, however, shows that it does reach 77.7%, which would indicate a high level of morphological similarity between these specimens. It highlights the magnitude of such variance as exists, in the context of the high level of morphological similarity between all specimens, (i.e. they seem to vary by similar amounts from each other). The mean value for similarity links within the two groups indicated above, is 81% (group 1) and 74% (group 2) respectively, defining the relationships between all possible combinations of individuals in the respective groups. Incorporated into this mean value are similarities between "distant" members of the same group, with lower values than the end members between groups. Additional evidence in this context is provided by the format of the similarity matrix (see appendix 1 - III).

The values in this matrix express in metric form, the degree of similarity which exists between any two individuals. The minimum value for any pair (i.e. the most dissimilar) is 132, between individuals 1 and 5 (see table 3 and appendix 1). The maximum value 823 expresses the relationship between specimens 1 and 17. The values of all

coefficients may be ranked according to their value, and this shows that there are values ranging throughout all the hundreds as follows:

100's = 2 200's = 5 300's = 5 400's = 12, 500's = 10 600's = 10

700's = 13 800's = 6 (see also table 3)

Values in excess of 80% exist between a number of individuals. In any one pair, one of the specimens is closely related morphologically to at least one other (although the level of similarity of the latter to the other members of the small sample may be lower). This situation appears to extend throughout the range of specimens analysed, which seems to consist of two remote end members i.e. 1 and 5, plus a continuously variable range of individuals in between, which gradually become more similar in form to a wider spectrum of specimens as they approach, presumably, the mode for those characters measured. The latter relationship is expressed in the "nearest neighbour" charts (appendix 1 - III).

The difficulty encountered in the placement of delimiting lines between this collection of specimens seems strong evidence that they form part of one continuously variable population.

(ii) Steneosaurus - Qualitative criteria

Three of the criteria used by Andrews (1913) to distinguish species of Steneosaurus are qualitative in nature: the form and relationship of the frontal and prefrontal bones, tooth form and number and scute form.

a. Frontal and prefrontal bones

The range in form of the nasal/frontal suture and its relationship with the prefrontals is illustrated diagrammatically in fig. 17, which shows that this feature is highly variable in its intricacy and shape, in the length of the anterior projection of the frontal and its level of termination relative to the most anterior point of the prefrontals. Andrews attached great importance to the above character, and at times used it as one of the major criteria upon which specific determination was based e.g. between S. hulkei and S. durobrivensis (Andrews 1913 p. 122)

and between S. edwardsi (Deslongchamps) and S. hulkei (Andrews) loc. cit. The former example also illustrates that Andrews could not have taken account of the individual variation that occurs in this character in the various specimens of S. durobrivensis; the similarity in form of the frontal/nasal suture of S. hulkei and S. durobrivensis R2865 in fig. 17 is notable. If, however, R2865 is compared with R3701 or R2073 (both S. durobrivensis), one sees sharp contrasts between all specimens. It should be remembered that Andrews would only have been able to compare S. hulkei and S. edwardsi by comparing the type of S. hulkei with a figure of the type specimen of S. edwardsi. On the basis of the above evidence, the synonomy of S. hulkei, S. edwardsi and S. durobrivensis seems probable.

b. Scute form

Among the lines of evidence used by Andrews to distinguish the species S. obtusidens from S. durobrivensis (and indeed the genus Mycterosuchus from Steneosaurus) is the form of the dorsal scutes. In S. obtusidens these are said by Andrews "to differ considerably from those of the other species" (of Steneosaurus) (1913 p. 133). "The pits are mostly shallow and elongated, they are arranged in lines radiating in the most case from the middle of the keel, and sometimes almost running together to form shallow grooves".(1913 p. 133).

The scutes of the type specimens of S. durobrivensis (R3701), S. obtusidens (R3168) and of a second specimen of S. obtusidens (R3169) were examined.

Many dorsal scutes are preserved in the collection for R3701, permitting an adequate study of the amount of variation for this particular feature within an individual specimen, the range being presented in pl.2bii. Unfortunately there are few scutes for specimen R3168, only one of which is actually figured in the catalogue (Andrews 1913), and so reference was made to the scutes from another specimen labelled as S. obtusidens by Andrews (R3169), so that a more accurate assessment of the variance could

be made (see pl. 2ai and ii).

Close analysis of the three scute series reveals that the elongate pits, so characteristic and notable in the figured S. obtusidens scute (Andrews 1913) pl. VIII fig. 6) are not universally present, or indeed representative of, other S. obtusidens scutes. From analysis of those associated with R3168, these scutes instead exhibit rounded pits, characteristic of the outermost border area of each scute. Passage inward towards the median scute border is accompanied by progressive elongation of the pits, a characteristic also noted in some S. durobrivensis scutes (see pl.2b). Towards the median border area S. durobrivensis scutes show elongated ovoid pits which become rounded in the proximity of the keel, and also in the outer border (see pl.2bi). In no case do the scutes of R3701 show the rather well defined radial grooves evident in the figured scute of S. obtusidens. Scutes belonging to R3169, however, although belonging to S. obtusidens, compare very closely with those of S. durobrivensis, differing only in the scale factor, which is the result of the absolute size difference between these specimens. R3169 scutes exhibit pits which vary in their degree of elongation with respect to their position on the scute and no development of radial grooves (see pl.2).

Analysis of scutes from specimens of S. obtusidens and S. durobrivensis housed in the Peterborough Museum also indicates that the amount of interspecific variation is not significantly greater than intraspecific variation for this character.

The figured scute from the type specimen of S. obtusidens (see above) is shown to be an inaccurate, atypical "representative" of those available for analysis, which illustrates only one aspect of a highly variable feature and is, therefore, taxonomically invalid.

Evidence provided from examination of modern crocodilian skeletons supports the view outlined above. Within individual specimens, a high

degree of variation in scute form occurs, depending on the position of the scute in relation to the body, and in the exact form of a particular part of an individual scute.

c. Tooth form and number

Material housed in Peterborough Museum throws some interesting light on this phenomenan. The pattern of tooth development in the specimens arranged serially below shows a progressive change in crown form, coincident with an increase in "massiveness" of the rostrum (which is indicative of an increase in skull proportions).

R39 (C.M.P.) shows similar crown form to R3168 (B.M.(N.H.)

R175 (C.M.P.)

R178 (C.M.P.)

R1 (C.M.P.

R2705 (B.M.(N.H.)

R3701 (B.M.(N.H.)

crowns becoming less blunt and size of snout decreasing progressively. It seems reasonable to suggest that an increase in the size/massiveness of the snout is correlatable with an increase in the bluntness of the tooth crowns. Specimens R175, R178, R39 (all from C.M.P. collection) show small differences in the size of their rostra, an indication of which is given in the values for the width of the snout at the anterior end of the nasal bones (this being the only measure of skull proportions that can be taken on all three skulls) R178 = 81mm, R175 = 82 mm and R39 = 86mm. Their teeth show an overall trend to increasing bluntness of the crowns with snout size, but this trend is complicated by individual differences in tooth character within the jaws of individuals of approximately the same size (see pl. 3). So there is some variance which is independant of any general trend in tooth form, and superimposed on that trend. There are two components, therefore, contributing to the pattern of variation

observed i.e.

Individual + Ontogenetic variation = total variation

In R3701 and R3168 (both B.M.(N.H.) we see individuals widely separated in terms of "massiveness" of the rostrum, with accompanying disparity in tooth crown form (see pl. 4). Specimen R2705 (B.M.(N.H.) gives the first indication of the progressive change in tooth form, as do certain of the replacement teeth in R3701 (see pls.4,5). Also important in this context is specimen 19.96.G12.a. from N.M.W. Cardiff showing tooth crowns intermediate in form between S. durobrivensis and S. obtusidens (see pl.7). The specimens from Peterborough and Cardiff complete the sequence for which Andrews examined what we might call the "end members". He based this taxonomic criterion on what he believed to be a distinct character showing discontinuous variation, but what we can now recognise as end members in a continuously variable feature.

These two characters, tooth bluntness and massiveness of the rostrum, are cited by Andrews as the main diagnostic characters which distinguish between the species S. obtusidens and S. durobrivensis. The above appraisal of these characters indicates that, while it may well be true to link development of snout and tooth form together, this character combination shows a high degree of individual variation and is a continuously varying character (for which functional significance may be suggested (see Kvam 1958), and as such cannot be considered a valid specific criterion. The cited characters are present, the relationship appears true, but it is the type of character, i.e. the way in which it varies, which makes it unsuitable for taxonomic purposes.

Examination of the above character has been important in two ways:

i) to re-examine the validity of tooth form and snout massiveness as specific criteria

ii) to examine possible functional relationships between these two characters. It seems reasonable to assume that the change in snout

and tooth form reflects a trend towards dietary specialisation. Such dietary specialisation can remove individuals sharing similar morphologies from direct dompetition with each other (see Dodson's thoughts on niche partioning of large reptiles 1975). This aspect has important implications on the "biological competition" concept governing the spatial relationships of the steneosaur species.

Buffetaut (Reading V.P. Conference 1978) described ontogenetic changes in tooth form in his current research on Cretaceous crocodiles, which he interprets as a response to dietary change. The changes in form cannot, in his opinion, be attributed to the grinding of two tooth layers together, that is the crown form is not the result of facets of "wear", but is the direct response to dietary influence. Langston (1973) states "Dentitions are naturally sensitive in responding to dietary influences..... it may be added that crown shape varies between different regions in the same jaw, and that the shape of the teeth is known to vary ontogenetically in living species". (p. 269).

In view of the skeletal similarities in cranial and indeed post cranial characters evident in S. obtusidens, S. durobrivensis (and S. hulkei), the statements above, and the evidence presented in this section, there seem to be no significant differences betwen S. obtusidens and S. durobrivensis, while the differences between S. hulkei and S. durobrivensis have already been shown to be of individual rather than specific significance. Furthermore, as has already been shown, (p. 57), the characters said by Andrews to distinguish S. hulkei from S. edwardsi are not considered to be significant, and S. hulkei is considered a possible synonym of S. edwardsi.

Thus we have shown that, using qualitative and quantitative evidence, all species of Steneosaurus are indistinguishable from each other and, considering quantitative evidence, these are in turn indistinguishable from the single species of Mycterosuchus.

It is now proposed to analyse those qualitative characters which were used (Andrews 1913) to distinguish between these two genera.

(iii) Qualitative information regarding the separation of the genera Steneosaurus and Mycterosuchus

In distinguishing between the genera Steneosaurus and Mycterosuchus, Andrews made the following observations of a qualitative nature:

1. Cranial characters: Greatly elongated snout, sharply marked off from the cranial region of the skull, which narrows very rapidly immediately in front of the orbits; teeth slender though not excessively so; temporal fossae relatively smaller and especially shorter than in typical steneosaurs.

2. Post cranial characters: Fore-limb less reduced than in steneosaurs; both distal condyles well developed; neural spines in the middle and posterior caudal regions broad and high and deeply notched anteriorly and posteriorly; scutes much more massive than in steneosaurs.

Thus at generic level, a combination of both cranial and post cranial characters is used, as in the identification of the genus Metriorhynchus.

As already noted, the type specimen of Mycterosuchus is R2617 B.M.(N.H.) (specimen 11 in the computer programme), and the other specimen labelled as Mycterosuchus is S.M.1 (specimen 17 in the computer programme). The results of bivariate and multivariate analyses shows that specimen 17 (computer number) exhibits high levels of similarity to specimens belonging to S. leedsi when only cranial characters are considered. Specimen 11 (computer number) is linked at a high level to Specimen 17, but is not closely similar to the other narrow-skulled steneosaurs.

Examination of the features listed above provides information which can be synthesised with that obtained through quantitative analysis and outlined above. Differences certainly are apparent in the morphology of the post cranial skeleton, and in limb and body proportions. Those aspects considered (by Andrews) to be taxonomically significant will be

examined here.

The range in morphology of the humerus of specimens: M. nasutus R2617 B.M.(N.H.) A, M. nasutus 1 (S.M.) B, S. durobrivensis R3701 B.M.(N.H.) C, Mycterosuchus sp. 1 (M.B.) D can be seen in pl. 8 and provides the only source of information about this bone and the way in which its osteology varies between specimens belonging to the genus Mycterosuchus. 1 (S.M.) appears to be transitional in form, the plane of the distal condyles making an angle of approximately 70^{o} with the articulation surface on the head of the humerus. The ulna condyle is very flattened and this makes it difficult to decide whether it is equally developed with the radial condyle (as noted by Andrews for the type specimen). Due to the nature of preservation of the Oxford Clay specimen, this kind of evidence is unreliable and little importance can be attached to it.

Due to their nature of preservation, the neural spines of the caudal vertebrae in 1 (M.B.) cannot provide any substantial evidence for the presence or absence of anterior and posterior notching (see pl. 9). Plate 9 shows the only caudal vertebra with spine preserved for 1 (S.M.) which shows similar notching to that developed in R 3892 B.M.(N.H.) (pl. 9).

The scutes from S. durobrivensis (R3701) and S. obtusidens (R3168) and Mycterosuchus sp. (1 M.B.) show an increase in "massiveness" which corresponds with that in overall size of the animals, and analogous to that seen between scutes from S. leedsi and M. nasutus (R2617 B.M.(N.H.) (see pls. 10 and 2).

Variance in the supposedly taxonomically significant characters is thus shown to exist in the very restricted sample available for analysis. In this sample the relevant skeletal elements are missing in some cases, further reducing the level of comparisons beyond the point where any valid taxonomic conclusions can be justified.

METRIORHYNCHUS

(iv) Quantitative criteria

The information contained in Table 2 presents succintly that needed to quantify "similarities" between members in the population. Each character is designed to test the validity of a particular (presently accepted) taxonomic criterion. Information presented in this way permits accurate comparisons to be made between specimens of contrasting sizes.

Detailed analysis of Table 2, shows that characters 2 and 6 give an indication of discrimination of specimens into two groups. In the majority of specimens, character 2 shows reasonably clear disparity, with a few individuals whose values blur what initially seems a clear dichotomy. There is an erosion of differentials with the inclusion of these specimens (which, incidently, are in the main specimens located by the writer, and as such were not considered in earlier taxonomic studies). This pattern seems to be a metric expression of a situation in which, in terms of the characters measured, there are modal values adhered to by the majority of the members of the population and defining the diagnostic features. The specimens referred to above, which we can call the "end members", represent greater variation from the mode. Extreme variation may result in odd specimens showing greater metric affinity with members of another group (not necessarily another species), rather than modal members of the group with which they share many features in common. This is the situation with respect in particular to characters 2 and 6. All other characters measured showed greater "within group" rather than "between group" variation, the groups being erected on the basis of the discriminating characters outlined above, often with complex intermingling of values as, for example, in the case of characters 4 and 5.

Thus, in this analysis, all members of the population share common features which permit a visual perception of morphological similarity, a selection of which show varying amounts of overlap when analysed quantitatively. In addition, some individuals posses a character combination

or character combinations which sets them apart, so that groups of specimens can be recognised, and these may be specific characters, (e.g. characters 2 and 6). These characters together quantify an aspect of snout growth, 2 being a measure of the "width element or component" of growth, 6 an indication of the amount of antero-posterior elongation in relation to broadening, that has occurred during growth. The specimens which show broader skulls have a reduced element of growth concerned with elongation of the skull and, consequently, a reduced distance between the nasals and premaxillae (since the expression of antero-posterior elongation is the extension of the maxillae. In narrow-skulled crocodiles, all the growth is concentrated in the antero-posterior extension and all "narrow-skulled" metriorhynchids have substantial separations between nasals and premaxillae (see Table 2).

A pictorial presentation of the character combination analysis can be effected by construction of a series of bivariate and trivariate plots (figs. 18 - 22), and these support the grouping of specimens as suggested above.

$$\frac{W/L \text{ at outer angles of the prefrontals in mid dorsal line}}{\text{Total skull length}}$$

and

$$\frac{\text{distance separating nasals and premaxillae as a \% of nasal length}}{\text{Total skull length}}$$

give the clearest indication so far of grouping based on the relationship between the degree of antero-posterior elongation, and degree of widthways expansion (i.e. are visually expressing characters 2 and 6 (see Figs. 19 and 20).

These results are certainly not compatible with the present taxonomic classification. A division into two groups, based on characters 2 and 6 seems reasonable at this stage in the analysis, but there is no evidence

for any major patterns within the two groups on the basis of those characters which can be analysed quantitatively (other qualitative characters will be examined in due course).

Examination of fig. 23, which plots values for each specimen on the first two axes or eigenvectors (see p.46), indicates a certain amount of clustering into three groups. The first group includes individuals (for identification see Table 5) 35, 29, 30, 27, 32, 31, 33. A larger group, group 2, in the centre of the graph, contains individuals 41, 38, 40, 23, 46, 44, 42, 18, 7, 5, 10, 26, 47, 20, 22, 6, 21, 49, 12, 8, 17, 25, 45, 43, 36, 39, 37, 4, 9. Finally, a more loosely clustered group, 3, includes individuals 19, 13, 14, 1, 3, 15, 11, 16, 2, 24, 48, (34, 28?), (the relationship of the last two specimens to groups 2 and 3 is problematical).

The graph is interpreted in terms of characters possessed by the specimens, in view of their spatial relationship on the eigenvectors. The separation between groups 1,and 2 and 3 is fundamentally based on breadth and narrowness of the skull. This situation is complicated by the relationship of individuals 28 and 34 and the relationship between groups 2 and 3.

Absolute size seems to be an important consideration in explaining distances between groups 2 and 3, and also the position of 28 and 34. These relationships are expressed as similarity levels in fig. 24. This indicates that a large percentage of group 2 are linked by levels of greater than 950 (values taken from the similarity matrix: see appendix 1). Individuals 18, 46, 44 and 42 within this group seem to represent a small divergence from the characters possessed by specimens grouped closely around the "norm" for this population. Their relationship with the rest of group 2 and, indeed, with the rest of the population, is measured in terms of the set of characters they possess, and the lower level of the similarity coefficient (940 - 949) expresses greater variance of these characters in specimens 18 - 42.

Group 1 shows an apparently lower level of similarity between its members. This results from the fact that there are far fewer individuals to compare with each other in this group, with the resultant less likelihood of attaining high levels of similarity, i.e. there is less chance for specimens to approximate to the mean for a given character. If there was an increased sample size, the situation illustrated in group 2 might be approached. The levels of similarity between individuals in group 1 (and the other groups) may be obtained from the nearest neighbour score charts (see appendix 1). End members of groups 1 and 2 are in fact linked at a relatively high level of similarity - see link between 42 and 35 for instance (806). The characters which seem to be the most significantly variable in groups 1 and 2, i.e. width of skull and size (length), are examined in fig. 25. The method employed involves the production of a ranked series, ordinating individuals whose preservation permits the measurement of the width between the outer angles of the prefrontals and which possess a sufficient portion of their skull to enable an estimate of total dorsal length to be made, and so increase the working sample size. A width index can then be calculated as follows:

W/L = width index, the rank being determined by the measured or estimated skull length (in dorsal mid line) the longest skull being given the rank 1. The width index can then be plotted against the rank values (see fig. 26). All individuals have been plotted, but of particular interest are the specimens which plotted in group 3 in figs. 23 and 24. These fall on the extreme right of fig. 26. This graph indicates that "shape" (i.e. the breadth of the skull, defined for the purposes of this graph by the width index) is independant from length (defined in this instance by rank values).

The most important factor contributing to the pattern of grouping seen in groups 2 and 3 (see p.66), seems to be size (length) (see fig. 25) and the values of the links between the end members of these two groups,

(940 - 949) suggest that the groups should be amalgamated. Although it is reasonable to assume size to be an indication of growth, there is no evidence, such as skull proportions or suture closure, to suggest juvenile status for any of these skulls. Specimens in groups 2 and 3 represent a set which, although variable in size, share similar morphologies, most importantly in those characters relating to skull breadth (which, according to the results of this analysis, seem taxonomically valid).

The width index graph (fig. 26) shows that individuals 28 and 34 are "broad-skulled" specimens, and their relationship to members in group 2 needs to be re-examined. A partial explanation of their position is provided by their size, which tends to place them close to other small skulls in group 2. It also appears true that, coincident with an increase in absolute size, there is a progressive divergence in skull "shape" (i.e. width) so that, on attainment of the size of members of groups 1 and 2, maximum disparity in shape results. There is, however, sufficient disparity in the shape of skulls of 28 and 34, to permit identification of the group (in terms of 1 or 2) to which they belong, i.e. group 1 (see evidence from figs. 19 and 20).

The relationship (i.e. similarity values) between the metriorhynchids which plot to the left of line 1 in fig. 26 is shown in figs. 30 and 31. Fig. 30 highlights the levels of the similarity coefficients between members of the "broad" and "narrow-skulled" groups. It also shows that the similarity levels progressively decrease as one compares more distant members of these two groups, until the lowest value is reached (between 41 and 27 = 175).

Fig. 32 shows that even when the size range for the metriorhynchid population is reduced by omission of the smaller specimens (i.e. lower ranks, figs. 25 and 26), clustering is still mainly a function of size (defined by skull length in mid dorsal line), linked with shape.

Thus we have seen that quantitative evidence permits the establishment

of broad and narrow-skulled groups which is in partial agreement with Andrews (1913). These two groups are at present subdivided using the following criteria:

(v) Subdivision of the narrow-skulled group

1. The relationship between the length of frontal anterior to the supra-temporal fenestrae and the least width between the orbits.

2. The number of teeth.
These are both quantitative criteria.

3. The relationship between the frontal and prefrontal bones.

4. Ornament of the dorsal skull bones.

These are both qualitative in nature.

The relationship between the length of frontal anterior to the supra-temporal fenestrae and the least width between the orbits is expressed in fig. 18, which shows that the amount of variance between individuals said to belong to the same species is considerable. Andrews erected this criterion on the basis of the sample illustrated in fig. 27, and for these few specimens there does appear to be a grouping. From the present study, however, it becomes evident that these individuals account for only a small percentage of the total variation.

The use of tooth numbers to aid in distinguishing species of metriorhynchids is totally unsatisfactory. This work reveals extensive variation in tooth numbers between individuals assigned to the same species by Andrews (1913), and even between right and left sides, or upper and lower parts of the jaw. Similar variations are recorded by Wenz (1968) working on the French material. Andrews (1913) states that M. moreli has 26 teeth in the maxillae, whereas M. superciliosum has 25. The number of teeth is not a significant factor in distinguishing between these or any other species, in animals exhibiting continual tooth replacement, such as Crocodilia.

The relationship between the frontal and prefrontal bones can be succintly

presented in diagrammatic form in fig. 28. The diagrams contained in this figure illustrate the degree of individual variation in this feature. They indicate that such a character should not be considered a valid criterion because of its extreme variation.

Both groups of specimens (groups being defined in terms of skull proportions outlined above) contain individuals which show a variety of degrees of development of cranial ornament, and collectively exhibit an entire spectrum of ornament development. (see pls. 11 and 12).

The end members of such a series can be established, and these specimens display virtually smooth, or conversely, very densely ornamented skulls. Within this range, however, it is impossible to distinguish positions at which it would be possible to draw significant lines of delimination which could be used as a basis for classification. Thus the type of variation displayed by this character (i.e. continuous) renders it invalid for taxonomic purposes. Andrews (1913) nevertheless devised such a classification based on this character.

It is proposed to elucidate in detail the development of ornamented cranial bone, in relation to the narrow-skulled metriorhynchids.

Wenz (1968) stated "It seems right that among the long muzzle forms we can recognise ornamented forms (M. superciliosum and M. moreli) and forms without ornament (M. laeve and M. leedsi) but to push the specific determination further hardly seems satisfactory..... in fact on most of the specimens examined the variations of ornamentation are minimal..... moreover there exists a range of intermediaries between the two extremes" (p. 31). Wenz suggested therefore that in those specimens displaying some ornament it was unsuitable for classification due to the nature of its variance. She distinguishes, however, between those with, and those without ornament.

The results outlined in this work partially agree with those put

forward by Wenz, but new evidence is presented which indicates continuous variation of this character between "smooth" and "faintly ornamented" skulls (see below). It is important to note that many of the specimens analysed by the writer (and others examined by Wenz) which display the ornament said by Andrews (1913) to characterise M. superciliosum have the cranial bone proportions that Andrews stated was typical of M. moreli! With respect to the development of ornament, specimens R72 and R7 (C.M.P.) are highly significant. Prior to the examination of these specimens, there had been little evidence available to support continuous variation at the "lower" end of the range i.e. between those specimens showing little or no ornament and those showing "moreli" type ornament. Specimens R72 and R7 (see pl. 13) provide strong evidence which favours definition of the nature of variation in the cranial ornament as continuous, rather than discontinuous or discrete, thus undermining its validity as a specific criterion.

Specimen R180 (C.M.P.) illustrates a pattern of development of cranial ornament in a smaller (probably younger) metriorhynchid, which can be compared with that of R2065 (B.M.(N.H.) in pl. 14 . This indicates that the development of ornament is independent of skull size.

(vi) Subdivision of the broad-skulled group

The second group formed in the initial division of the genus Metriorhynchus (see p.69) is subdivided at present into three species using the following criteria:

1. The degree of separation of the nasals and premaxillae.
2. Number of teeth.
3. The length of the rostrum.

These are quantitative criteria.

4. The relationship between the frontal and prefrontal bones.
5. The ornament of the dorsal skull bones.

These are both qualitative in nature.

Comparisons of the distances separating the nasals and premaxillae have been made in table 2 and figs. 20 and 22. These indicate a range of values in which the specimens with the broadest snouts (defined by the distance across the outer angles of the prefrontals) show the least distance of separation of the nasals and premaxillae. The separation of these bones as an expression of the degree of antero-posterior growth contrasted with that element of growth concerned with widthways expansion of the rostrum. In the widest skulls,growth has concentrated to a greater degree on expansion of the skull, with a consequently smaller amount of elongation (i.e. a smaller separation of the bones separated by the maxillae where antero-posterior elongation is reflected).

The results suggest that the distances separating the nasals and premaxillae are too variable to form the basis for a taxonomic criterion and that they do not adhere to the relationships expressed by Andrews (1913).

Research into the number of teeth indicates (for the restricted sample analysed) this feature to be unsatisfactory for use in classification. There are in all cases lower numbers of teeth in the jaws of the broad, as opposed to the narrow-skulled crocodiles, and this is in relation to the lower degree of antero-posterior elongation of the maxillae, which are the main tooth-bearing elements. It is possible that the number of teeth, in conjunction with the broadening of the jaws, relates to dietary change coincident with increase in overall skull/jaw size (and presumably the entire individual). This situation is documented in living crocodilians (Cott; 1961; Dodson; 1975). Here, the increase in the size and width of the jaws is related to a corresponding increase in the range in size of prey that the crocodile can successfully prey on. The question of probable prey in Callovian times, which would be analogous to small (and sometimes not so small) mammals preyed upon by large living crocodilians, remains problematical. If the metriorhynchids prey was largely restricted to invertrebrate benthos, nekton and fish, small in relation to the predator

jaws, the configuration obtained by the broad-skulled metriorhynchids is difficult to explain in terms of the living crocodilian morphs.

Cott's study (1961) brought to light the unexpected importance of the role of molluscs in the diet of a wide range of crocodiles of varying lengths (and presumably ages), where the volume of molluscs exceeded all other types of food organisms accounting for nearly 70% of the total. The importance of crustecea in the diet varied widely, while for crocodiles ranging in length between 2.0 - 3.5 metres, fish formed the main food and their relative importance can therefore be seen to change markedly with the length of the crocodile.

Thus the broad-skulled metriorhynchids have fewer, similarly shaped, but larger teeth than in their narrow-skulled counterparts (see M^{c}Ilheny 1976 for documentation of this situation in living crocodilians).

Assessment of the possible validity of using the length of the rostrum in a taxonomic sense is difficult because the relevant parts of the skull are preserved in only a few specimens. The available data suggests that this feature is variable, as is the situation in the narrow-skulled individuals, for which there is a much more comprehensive sample size. This character is not independent from the distance separating the nasals and premaxillae, because the length of the rostrum will be determined by the amount of antero-posterior elongation, expressed mainly in the length of the maxillae, (which in turn determines the separation of the nasals and premaxillae).

The frontal, prefrontal relationships are presented pictorially in fig. 28 illustrating their variability and hence unsuitability as a taxonomic criterion.

Ornament is mentioned in Andrews' type descriptions of M. cultridens, M. brachyrhynchus and M. durobrivense, although minor importance is attached to it, in a taxonomic sense, in the case of these species.

According to Andrews (1913), The degree of development of ornamentation varies between species, as does the amount of ornament on various cranial bones (namely the frontal, prefrontal and nasal bones) within a given specimen. This might be the effect of broadening the skull by increasing the width of the frontals and nasals so "dispersing" the density of sculpture of these bones. The existence of apparently continuous range of development of ornament in these forms is highly significant, lending support to the hypothesis for the existence of a similar range in the narrow-skulled metriorhynchids.

Of particular interest is the ornament on R3804 (B.M.(N.H.) - M. cultridens (see pl. 11e). This does not appear as strongly developed as Andrews concluded (1913 p. 196), and as such represents the least degree of development of ornament that has been recorded from a European specimen.

In this context, one of the characters used by de Gasparini & Diaz (1977) to define their new species M. casamiquelai, needs to be re-examined. "There is no ornamentation (all species in group (b) Wenz (1968) have different degrees of ornamentation") (p. 357). Unfortunately the actual specimen of M. casamiquelai is inaccessible, in South America, and comparisons are by photographs given to the author by de Gasparini(see pl. 15) and personal communication on this aspect of morphology with her. As far as can be discerned, there is a gradational development of ornament between M. casamiquelai and M. cultridens (R3804 B.M.(N.H.), which shows lateral pitting of maxillae and strias of the nasals. Similar pits appear on M. casamiquelai (see pl. 15) where faint striae are also evident in lateral view. An added complication is encountered, in that a portion of the frontal and prefrontal on M. casamiquelai has been restored, reducing morphological detail from a vitally relevant area of the skull. It would appear that M. casamiquelai supports the concept of a continuous range of variation in the development of ornament, and provides us with the very beginnings of ornament, as do the specimens R72 and R7 (C.M.P.)

for the narrow-skulled metriorhynchids (see p. 71).

Six of the characters used by de Gasparini & Diaz (1977) in the definition of M. casamiquelai (see p. 31) have been shown, by the results presented above, to be invalid for taxonomy, exhibiting a wide range of individual variation. They are very similar to characters used by Andrews in 1913 (whose work these authors have already critisied in the same paper) though they now use similar criteria to distinguish their new species.

One further character merits close examination "That the suture separating the premaxillary and maxillary bones has the shape of an M, all known species have the shape of a V" (de Gasparini & Diaz 1977 p.357). The shape of the premaxillary - maxillary suture was examined in specimens available to the author. Bearing in mind the variability of other cranial sutures, this character would not appear very suitable. Detailed examination reveals that some individuals of the genus Metriorhynchus do have an M shaped suture, and these are illustrated diagrammatically in fig. 29 (where A = R3699 - broad-skulled form, B = R6860 - narrow-skulled form and C = R2508 - narrow-skulled form, all in the B.M.(N.H.) collection). The V-shaped suture does certainly appear the most common, and this might explain the limited occurence of the M-shaped suture, particularly in the more limited sample of the broad-skulled metriorhynchids.

DISCUSSION

(i) METRIORHYNCHUS

Size-linked characters defining the shape of the skull (i.e. the width of the rostrum) are important, indeed are the only characters that can distinguish between two groups of metriorhynchids.

The data used in the multivariate analysis of this genus was not standardized for size because, when the size range was truncated by omission of specimens in the "lower" part of the range (i.e. all those

to the right of line 1 in fig. 26, clustering was still seen to be in part, a function of size-linked shape characters (see figs. 30, 31 and 32), (also there are very few complete skulls preserved to effect a standardization in the sample of metriorhynchids here analysed). In the steneosaurs, size was shown to have no relation to shape characters (see figs. 12 and 13). The size range in the metriorhynchids analysed does not include recognisable juveniles (see p. 68). The size range may be perhaps attributable to an age range, after the smallest skulls have lost the typically juvenile proportions (see Mook 1921a), but are still growing at a reasonably fast rate (Neill 1971 p. 264), the rate of growth is known to become very gradual with increased age. (Neill loc. cit. pp. 264, 265 and 269).

It appears that, during such a size/growth range, there is a progressive divergence in shape, which in the context of this work means a progressive broadening of the skull in individuals belonging to the group of crocodiles known here as the "broad-skulled group".

Interpretations of these facts may be as follows:

1. Interspecific

Two species are represented in the population (the "broad" and "narrow-skulled" groups).

Niche partitioning between them is not by size alone (Dodson 1975 on niche partitioning between large reptiles), but by changing dietary influences, which are reflected in progressive disparity in skull and jaw size and breadth, facilitating predation of an increased range of prey. (see Cott, 1961, table 19 and fig. 34, for different categories of food taken by crocodiles, in relation to their length).

The variation encountered in the population embraces that resulting from age, sex and functional requirements, which may alter during ontogeny, and other dimorphisms (encountered in recent crocodilian populations, for which no explanation has yet been offered, Neill 1971, pp. 180 and 181, fig. 64).

2. Intraspecific

The observed dimorphism is due to intraspecific variation in skull shape and proportions. Evidence in support of sexual dimorphism within species comes from Cott (expressed graphically in 1961 p. 252, fig. 16), Neill (1971) pp. 243, 250 and fig. 85, M^{c}Ilheny (1976) p. 64. Males are noticeably larger than females (which might be expected to be reflected in the fossils as larger skulls (see Greer 1974), in which case females would correspond to those specimens which plotted on the bottom left area of the principal coordinate graphs i.e. group 3 (see p. 66 and figs. 23 and 24). The delimiting line between males and females is, of course, somewhat ill-defined. The males would correspond to the remainder of specimens on these graphs. The explanation of the broad-skulled group, in this instance, would be that some crocodiles (males?), on reaching a certain skull length, broaden out rather than elongate, a situation which is documented in the literature for living crocodilians (Neill 1971, p. 180). The evidence in the literature always refers to this phenomenan as occuring in males, but with no statement to the effect that it is exclusive to this sex.

Neontological morphological criteria, therefore, provides evidence that the disparity in skull form, encountered in this population, could be an expression of variation at intraspecific level.

(ii) STENEOSAURUS

Certain characters, quantified by the present work and previously regarded as taxonomically significant, have been shown to be invalid because they are highly variable.

Standardization of multivariate data has revealed variance due to "shape" characters which, by reference to the bivariate analysis, might be defined as the relative proportions of the snout or rostrum to the overall length of the skull, or the width or "massiveness" of the skull and rostrum. The former character combination was the only one which

permitted any kind of division between individuals 1, 2, 3, 17 and 11 (computer numbers - see table 4) and the remainder of the population (see table 1). All other characters measured showed varying degrees of overlap, or wide ranges of variation (see table 1). Character 1 in this table supports to some extent separation into two groups, the first to contain specimens 1, 2, 3, 17 and 11 (see above), and the second the remainder of the specimens analysed. The range of this character within the former group is 3.27% and within the second 5.9%. The minimum between-group variation is 7.4%, between end members of the two, i.e. the most "alike" specimens from the two groups. These values are very important. There is, in fact, a very small difference in within-group and between-group variation, and such an amount might be explained by factors affecting the preservation of the fossils. When dealing with figures on the scale of those outlined above, effects resulting from fossilisation must be taken into consideration, in addition to experimental error, which raises some doubts as to the significance of a division based on such a scale of figures. The various lines of evidence presented in this work may indicate that the steneosaurs analysed represent a cline of continuously varying individuals, and therefore any attempt to quantify or measure the "similarity" between an individual at one end of the range, and all the others, will result in a graduated scale of ever-decreasing values, from the most "alike" pair, to the most "unlike" specimens occupying opposite ends of the cline. These individuals will be very unlike most others in the cline and will have low similarity matrix values with respect to the majority of members in the cline, (see appendix 1 - III).

Bivariate and multivariate analyses have shown there to be very obvious differences between end members (if we consider this selection of individuals to represent a cline). This difference, however, is whittled away with the inclusion of members of the series which are morphologically more closely related, until a stage is reached when the disparity between the

hypothetical groups 1 and 2 (see p. 52) has dwindled to such an extent, that the difference between the most closely related end members of the two groups is less than the difference between the end members of either of the groups. This means that, if we are making a visual comparison between specimens distantly placed in the cline, in terms of their morphology, they will be distinctly different, but comparisons between nearly related members will show these differences to have merged, almost to imperceptibility.

One would expect a different format for the similarity matrix if there was reasonable evidence for a separation of steneosaurs into two or more groups. It would show a cluster of high values (the within-group similarities), in conjunction with an amount of low values indicative of the "between-group" similarities.

The relationship between specimens 11 and 17 (see table 4), at present classified as M. nasutus, and the other steneosaurs is problematical. Consideration of the information available at present, suggests that there are no grounds for separating these two from "S. leedsi type-skulls", and that the features designated as of generic and specific importance by Andrews (1913) are individually variable, showing extreme variation in these two skulls.

At present, with the limited material, it is not possible to be decisive about the post cranial skeletal characters which have been under discussion, i.e. those which have been used in the definition of the genus Mycterosuchus. Minor variation does exist in the morphology of certain bones and, in view of the lack of available data, these should be recorded, in the hope that they can be useful by providing information which may lead to a solution to this problem by future discoveries of material. The author suggests reversion to the original name given to this material by Andrews in 1909, Steneosaurus nasutus.

Whether morphological differences on the scale of those outlined in

this work can really be used to define or delimit a specific boundary, or any other type of boundary is highly controversial. In this instance it seems that we are oversplitting, and using the flimsiest lines of evidence and the difficulties encountered in any attempt to place specific boundaries is an indication of the falseness of imposing such boundaries at all. It seems wise to acknowledge such morphological differences as exist, noting their magnitude, and present the facts accurately, without overemphasising the importance of the differences in respect of the similarities.

It seems reasonable to present the following possible explanations for the results outlined in this work:

a) That the specimens in question represent two morphologically similar species, (i.e. specimens 11, 17, 1, 2 and 3, and the rest of the sample - see multivariate data and table 4), with possible dietary differences between them, being reflected in the type of teeth and proportions of the skull and in particular the rostrum, (Cott 1961, Iordansky 1964, Neill 1971, Dodson 1975 and Langston 1973), niche partitioning being dependent on this.

b) These specimens represent a cline of individuals, of one species only, comprising specimens of all ages (age is presumed proportional to size), both sexes (which are indeterminate), and in which some of the morphological differences can be attributed to dimorphisms (which are documented, but as yet unexplained in living crocodilians) (Neill 1971) and dietary change with ontogeny, (this is well documented in the literature e.g. Cott 1961, Neill 1971, Dodson 1975 and M^{c}Ilheny 1976).

CONCLUDING STATEMENTS

In view of the difficulty encountered in attempting to identify convincing discriminatory characters, the following revisions to the

presently accepted taxonomy of the Callovian steneosaurs are proposed:

That only one species can be distinguished, and that this will include all Callovian species of Steneosaurus, and embrace those specimens presently included in the genus Mycterosuchus.

The next problem involves the choice of the type specimen and species. On the basis of evidence presented in this study, the synonomy of S. edwardsi with the rest seems possible. Characters isolated from E. E. Deslongchamps' original descriptions (1867) by Andrews in 1913 as being taxonomically significant i.e. those which could be used to distinguish between S. edwardsi and his Callovian species, have been shown to be invalid. This effectively destroys the basis of Andrews' and E. E. Deslongchamps' diagnoses. Because of the destruction (during the last war) of material from which the diagnosis of S. edwardsi was made, any comparison between the type specimen of S. edwardsi and the Callovian steneosaurs from England must necessarily be by comparing the type English species with a figure. There are no records of suitable material from similar stratigraphic horizons in France, which could be designated the holotype. One cannot, therefore, be absolutely certain that the proposed or probable synonomy is correct.

It is important to record the existence of the figure and description of the senior steneosaur species, S. edwardsi whose relationship with the steneosaurs examined in this work remains problematical.

The name chosen for the Callovian steneosaur species is, therefore, S. leedsi (Andrews 1909).

Diagnosis of the species

Rostral portion of the skull varying in robustness and length, preorbital length ranging from 73% to 52% of the whole skull length. Considerable variation in the degree of separation between the nasals and premaxillae, although these bones are never in contact with one another. The relationship between the position of termination of the frontal and

prefrontal bones anteriorly, and the form of the frontal/nasal suture also shows extensive variation. Variable tooth number, some teeth show a change in crown form i.e. an increased bluntness, coincident with the increase in size of the skull. Symphysial region of the mandible occupies between 42% and 58% of the total jaw length. All specimens possess scutes, with pits which range in form between elongate and rounded, and which vary in their form and arrangement to each other within individual scutes and depending on the position of a particular scute on the body.

Slight variation in the osteology of the proximal part of the humerus, and in the proportions between the propodals and epipodals in the fore and hind limbs occurs at individual level.

The range of cranial morphology incorporated in this species is shown in pls. 16 - 18.

METRIORHYNCHUS

Diagnosis of the species

In this genus it is proposed that there are two species, which can be distinguished on the basis of their skull proportions i.e. breadth, the distance of separation between the nasals and premaxillae and tooth number (which are the result of increased widthways expansion of the skull in relation to antero-posterior elongation).

Individuals belonging to the first species possess the following characteristics:

Narrow skull, with many close set pointed teeth. Frontal and prefrontal bones show extensive range in development of sculpture and in the relationship between their most anterior point of projection. The nasal/frontal suture displays a variety of forms. The development of the frontal bone, as illustrated by the relationship between the width of the bone between the orbits and its length in front of the supratemporal fenestrae, is shown to be individually variable. The nasal and premaxillary bones are separated by varying intervals, but are never in contact with one another.

The name chosen for this species is the oldest (in a chronological sense) name for a Callovian narrow-skulled metriorhynchid - M. superciliosus (M. superciliosum de Blainville 1853 emend. E. E. Deslongchamps 1867, revised species name ending in agreement with Buffetaut (1977) (see p. 31).

Individuals belonging to the second species possess the following characteristics:

Broad skull (defined by the width across the prefrontal bones) in relation to total skull length, with verying amounts of sculpture on the frontal and prefrontal bones. These bones vary in the relationship between their most anterior point of projection. The nasals and premaxillae are in contact with one another in some individuals, while in others they are separated by a variable but considerable distance (but in the majority of cases this distance is less than the distances found in the narrow-skulled species: M. superciliosus. Teeth are fewer in number than in M. superciliosus, but have similar pointed crowns.

The name chosen for this species is the oldest (in a chronological sense) name for a Callovian broad-skulled metriorhynchid - M. brachyrhynchus (E. E. Deslongchamps 1867).

The range of cranial morphology in M. superciliosus is shown in pls.22,23 and in M. brachyrhynchus in pls.24, 25.

MODE OF LIFE

INTRODUCTION

Until the present study, the skeletal elements of Callovian crocodiles have been considered largely in terms of their morphology, and treated as "shapes" of bone, in isolation from the attachments they provided for muscles and without regard for forms of articulation, possible directions of movement or orientation of limbs. They are meticulously described and figured in Andrews (1913). Neontological-palaeontological comparisons have been largely overlooked, with the exception of Kalin (1955), Krebs (1962) and Langston (1973). Other isolated pieces of work have attempted to link the "form" and "functional" concepts with varying degrees of thoroughness e.g. Fraas (1902), Andrews (1913), Steel (1973), Buffetaut (1977) and Buffetaut & Thierry (1977) but the nature of these works is superficial. Examination of neontological material in the course of this study has also revealed the need for revision of some areas of post cranial myology.

It is important to re-examine the existing osteological descriptions in conjunction with available myological data. This can be synthesised with new evidence presented in this work on both of the above aspects and also on the ecological situation in the Callovian crocodiles, in an attempt to forge linkages between the static "form" and the dynamic "function" of these animals.

BIOMECHANICS - SOME PRINCIPLES

During locomotion elements of the skeleton act as rigid levers which are operated by the limb muscles about their joints and are, therefore, amenable to analysis by Newtonian mechanics (Gray 1944). These lever systems comprise: Fulcrum (pivot), effort and load

The design of the lever system can vary in terms of the relationships of the above elements and they are classified accordingly as 1st, 2nd or 3rd order lever systems (fig. 33A). In the first order systems the fulcrum (represented in the skeleton by the joint) is in the centre, with the muscle attachment (the effort) at one end and the load at the other. In a second order system the load is situated between the pivot and the effort. In a third order system the effort is positioned between the pivot and the load; this is the most important lever system in relation to limb movements.

It is possible to apply other mechanical considerations to the way in which the skeleton moves, thereby treating the body as a machine through which the muscle force is applied ("A machine is a device for applying forces" Alexander 1968 p. 13). Lever systems can considerably modify forces produced by muscles and the resulting forces can be calculated using basic mechanics, e.g. application of a force (F_1) to one part of a machine results in the machine applying a force (F_2) at another (Alexander 1968). A small force at one end of a lever can be made to produce a much bigger force near the fulcrum (as shown in fig. 33B) by taking moments. The ratio F_1/F_2 is known as the mechanical advantage of the machine. The distance F_1 has to be moved in order to move F_2 a unit distance is known as the velocity ratio (d_1/d_2 in fig. 33B). In a perfect machine the mechanical advantage would equal the velocity ratio, but in real machines it is always less (owing to friction at the fulcrum, for instance). The mechanics of limb motion can be studied using these principles. A comparison between the mechanical advantage of the fore limbs of a horse and armadillo is shown in fig. 34 (after Alexander 1968, who applied the work of Smith & Savage 1956). The line of action of the M. teres major (one of the main limb retractors, see table 12 is illustrated by line M, where h = the vertical distance from the fulcrum to the ground (the resistance arm of English 1977) and l, the distance from

the fulcrum to the line of action of the M. teres major (moment arm, English 1977). The M. teres major exerts a force (F_1) (the reaction force, English 1977) on the humerus, the moment of force of this about the glenoid (fulcrum) can be expressed as (F_1l). It causes the foot to exert a force (F_2) on the ground, and the moment about the glenoid is (F_2h) (the propulsive force of English 1977). The resistance from the ground causes the body to be propelled past the limb. In water, the reaction of the water on the limb contributes to the production of that thrust (English 1977). If no friction existed at the fulcrum these moments would balance i.e. $F_2/F_1 = l/h$ i.e. M.A. = V.R.

The horse is adapted for rapid leg movement but does not need to exert a large force on the ground. The former requirement necessitates a low velocity ratio and the latter means that the animal can tolerate the low mechanical advantage that is a consequence of the former. In the horse the ratio approximates to $l/h = 1/13$ (Alexander 1968).

In contrast, the armadillo uses its front legs for digging so that it is necessary to impart large forces against the ground. To do this requires a high mechanical advantage and also the means to accommodate the accompanying high velocity ratio i.e. $l/h = 1/4$. The velocity ratio indicates the extent of conversion, by geometry, of the effort of the muscle into muscle force (English 1977).

There are a number of ways in which the mechanical advantage of a limb might be increased:

a. by increasing the volume of the associated muscle

b. by decreasing the moment arm of resistance (h in fig. 34)

c. by increasing the distance between the insertion of the muscle and the fulcrum (i.e. altering the line of action of the muscle and thus affecting distance l in fig. 34)

Decreasing the relative length of the proximal segment of a limb (i.e. l) has the effect of decreasing the mechanical advantage (i.e. in the example

of the horse in fig. 34A $\frac{x1}{h} = \frac{1}{h}$ (M.A. = V.R.) expresses the need of the M.teres major to shorten by this amount to move the foot through a distance x relative to the body). This adversely affects the power but improves the speed of the limb.

A knowledge of the type of lever system, types of joints involved and the points of insertion of the muscle on the skeleton, is of great importance when attempting to understand the forces involved and mechanism of limb action during locomotion (Goldspink 1977 p.9). It seems possible to see a correlation between the adaptation of mechanical advantage and different habits. It is also possible to demonstrate these principles in other animals, and with other parts of the body (Alexander 1968) and they have been applied to crocodilians for the purposes of this study.

BIOMECHANICAL SITUATION IN RECENT CROCODILES

(i) THE SKULL

As can be seen from table 7 and figs. 35 and 36, crocodilian jaw adductors insert very closely to the jaw articulation in relation to the length of the jaws. The length of the jaws is increased by the quadrate bones which are inclined posteriorly. A consequence of the position of the adductors is their low mechanical advantage, and a consequence of the length of the jaws is a very large gape. The animal needs to exert a great force, however, using these muscles to catch and kill its prey (Iordansky 1964).

Smith & Savage (1959) analysed the loads applied to carnivorous mammal mandibles and correlated the differences in the shapes of the lower jaws and relative sizes of jaw muscles with the ways in which mammals use their jaws for different feeding habits (see fig. 37, after Alexander 1968).

Iordansky (1964) believed similar loads were applicable to crocodilian mandibles and the forces that were imposed on the jaw were as follows:

a. Force applied by the fourth anterior teeth of the mandible, which are the equivalent of incisor and canine teeth in the mammals, when the prey is seized. The force so created acts on the front of the jaw and has a forward component (generated by the escaping prey) and a downwards component (the upper jaw pressing on the lower one). The resultant will act as shown in fig. 35a and b (after Iordansky 1964), P_1

b. Force applied to the middle of the mandible, directed vertically downward and generated through grinding and cutting action of the teeth, shown in fig. 35c as P_2 (after Iordansky 1964).

The lines of action of the jaw adductors are included in these figures to summarise the situations at closed jaws and widest gape (i.e. fig. 35a, 35c and 35b respectively). Iordansky represents the forces and lines of action by vectors in these diagrams i.e. a given force, acting at a given point on the jaw, is represented by a line drawn outward from that point in a given direction and the length of line represents the strength of the force. Thus in fig. 35 the solid arrows represent the lines of action of the muscles and their length is indicative of the minimum force applied by each muscle to retain the jaws closed. Iordansky calculates these forces from a parallelogram of forces as follows:

i. one side of the parallelogram corresponds to the load applied to the mandible i.e. P_1 or P_2

ii. the other side lies on the line of action of the muscle

iii. the diagonal of the parallelogram lies on the line of action of the resultant of the load and force of muscular contraction, and this straight line must pass through the fulcrum

He also notes that the mechanical advantage of a muscle is inversely proportional to the minimal force of muscle contraction necessary to

retain the jaw closed. The dashed lines (fig. 35) show the loads applied to the jaw joint when a given muscle contracts and their length represents the resultant of P_1 and adductor contraction. (Compare with the diagrams of mammal jaws for simplified presentation of these forces in fig. 37).

The forces of contraction of the jaw adductors are composed of horizontal and vertical components, which tend to draw the mandibular rami upwards and inwards with great force during adduction of the jaws (see fig. 12 p. 270 Iordansky 1964). The medial displacement of the rami is prevented by the projecting pterygoid "wings" (see pl. 26), which limit their movement to the vertical plane and restrict the horizontal component. This protects the mandibular symphysis which has a relatively small surface area in relation to the jaw length. The fibrous anterior part of the stem tendon (see table 7) acts as a buffer between the lateral edge of the pterygoid wings and the mandible when the jaws are adducted and abducted (Iordansky 1964).

The muscles attached to the stem tendon (see table 7), the M. adductor externus profundus and the M. pterygoideus anterior have the largest mechanical advantage of the adductors, because the moment arms of these muscles about the fulcrum are greater than the others i.e. the distance between the effort and fulcrum (line of action of the muscle and jaw articulation) is greater. The M. pterygoideus anterior maintains the largest mechanical advantage for both positions of close and wide gape. The muscle fibres and stem tendon can maintain a highly advantageous mechanical position in relation to the fulcrum at every jaw position by slipping over the lateral edges of the pterygoids. The distance and direction of lines of action (from the fulcrum) of the other adductors will be modified according to the degree of abduction (for an example of this see the function of M. pterygoideus posterior at wide angles of abduction in fig. 35b). The M. adductor externus profundus possesses an inverse correlation with the development of the above muscle. It is

extremely well developed in long snouted crocodilians which show minimal development of the M. pterygoideus anterior. Short snouted crocodilians show the combination of maximum development of the M. pterygoideus anterior and weak development of M. adductor externus profundus.

These muscles have contrasted functions, caused by differences in their position in relation to the fulcrum and load in the lever system, and reflected in the volume of the muscles in a particular animal. The line of action of the M. pterygoideus anterior, a consequence of its position of origin and insertion, is most distant from the pivot, with a large mechanical advantage at all angles of gape (Iordansky 1964). The line of action of the M. adductor externus profundus passes closer to the fulcrum (pivot), producing rapid but relatively weak movements, advantageous at small angles of jaw abduction (Iordansky 1964).

Crocodiles which feed on prey of varied size, including large items, will require powerful adductor muscles (i.e. high mechanical advantage at all angles of gape). These crocodiles are known to exhibit shorter jaws and show maximum development of the M. pterygoideus anterior. Those feeding on small swift prey (and sometimes exclusively on fish) require rapid jaw closure and small angles of abduction are sufficient. They have longer jaws and show maximum development of the M. adductor externus profundus. This seems to be an example of adaptation of mechanical advantage to predation (see p. 85). The degree of development of the M. adductor externus profundus is reflected in the dimensions of the supratemporal fenestrae (Iordansky 1964) and, in conjunction with the proportions of the cranium and jaws, can give an indication of its development and the mechanics of jaw systems in fossil crocodilians.

The M. intramandibularis has a rather different function from those muscles inserting dorsally on the stem tendon (see table 7). Crocodile jaws are opened by the M. depressor mandibulae, which is a relatively weak muscle. (Iordansky 1964). These animals are known to be able to sustain

their gaping jaws during lengthy periods of basking, however, and during the pursuit of fish. When the gape is wide, the pterygoid flanges are displaced from under the stem tendon, to occupy a position anterior to and above them. Contraction of the M. intramandibularis (with the dorsal adductors simultaneously relaxed) will draw the stem tendon forwards and downwards, so fixing the position of the jaws, because the pterygoids are prevented from moving by the stem tendon. At adduction of the jaws, the dorsal adductors contract and draw the stem tendon upwards, the pterygoids will slip under it, permitting the jaws to close (Iordansky 1964).

When the jaws are nearly closed the line of action of fibres of the M. pterygoideus posterior which insert on the angular, is distant from the fulcrum, a function of the large mass of this muscle. With the jaws in this position this muscle has a large mechanical advantage as an adductor. Those fibres which insert on the retro articular process pass close to the fulcrum, with a corresponding small mechanical advantage, and their function is to prevent disarticulation of the mandibular joint. When the gape is wide, the entire muscle has the latter function, because the line of action of the muscle passes close to the pivot (Iordansky 1964).

The line of action of the M. adductor posterior passes very close to the fulcrum and has a correspondingly small mechanical advantage as an adductor. Its function is to prevent disarticulation of the jaw.

Thus these two large muscles prevent dislocation of the mandible joint by the application of loads when large prey is caught.

The M. adductor externus superficialis and the M. adductor externus medius have a small mechanical advantage according to Iordansky (1964) and the overall power of the adductors is increased by their action.

Skull characters relating to the attachment of jaw muscles and the mechanics of feeding in crocodilians were examined by Iordansky (1973), who categorised them as primary-mechanical, and secondary-muscle characters. He provided detailed descriptions and illustrations of the above (plus a bibliography).

Detailed examination of instances of analogous adaptations between mesosuchians and eusuchians, in terms of Iordansky's primary and secondary characters, in conjunction with data from other works, notably Adams (1919), Chiasson (1962), Iordansky (1964), Dodson (1975) and Langston (1973) can provide a rationale for the interpretation of the Callovian crocodiles - "the specialisation in crocodilian cranial design as seen in fossil crocodilians" (Langston 1973 p. 264) (for these interpretations see pp.116 - 120. It is apparent (see p. 90) that a close correlation exists between jaw form, size of the supratemporal fenestrae and mode of feeding in living crocodilians. There are also correlations between the jaw structure and degree of development of undulations of the jaw margins and type of dentition (Iordansky 1973). These characters apparently assist in holding and manipulation of captured prey (large in relation to the size of the jaws), clamping it firmly and, in doing so, partially compensate for mechanical disadvantage of their long jaws (Iordansky 1973). Analogies which can be introduced here to illustrate the effect of the undulations would include tissue forceps and pinking shears. Maximum development of the undulations is seen in short snouted species, which are known to feed on a variety of larger prey, including some terrestrial animals (Cott 1961, Iordansky 1964, Neill 1971, M^{c}Ilheny 1976), and their absence in fish eating gavials would seem to support the above conclusion.

Iordansky (1973) suggested that the development of the pterygoid wings was related to their function i.e. preventing medial displacement of the mandibular rami (in conjunction with the action of the M. intramandibularis). This action would result from the medial component of forces induced by mandibular adductors (see table 7), and prevention would necessitate the development of long, steeply inclined pterygoids in the species where the gape is wide (e.g. Alligator and Caiman). In long snouted forms (e.g. Tomistoma and Gavialis) they show minimal development, which is apparently adequate to prevent displacement of the mandible at narrow gapes; Iordansky(1973) presents a selection of illustrations

showing the variation in the development of this character (loc. cit. figs. 3e, 4e, 5e - 7d, also see here pl. 26.

(ii) POST CRANIAL

An investigation into the sites of origin and insertion, and anatomy of limb muscles in living crocodilians has provided the following information:

a. It has verified the available literature, and led to some revision.

b. It has presented some new information in diagrammatic form.

c. It has provided a neontological model, which can serve as the rationale for the reconstruction of the myology of the Callovian crocodiles. The character of the areas of origin and insertion, and the development of associated muscles in the neontological material examined can provide some insight into the apparent development of the same in the fossil, as indicated by the expansion or reduction of the corresponding bony areas for muscle attachment.

d. It can, in conjunction with osteological and articulary details, provide the basis for a mechanical analysis of limb motion.

METHODS

The limb muscles were investigated by dissection of three specimens of Caiman sp.

(iii) PRESENTATION OF RESULTS

PELVIC MUSCULATURE

The positions of the dorsal and ventral pelvic musculature, their relationships to each other and sites of origin and insertion have been verified with the results shown in Haughton (1864-68), Romer (1923) and Chiasson (1962).

Their sites of origin and insertion and actions (after Chiasson 1962)

are listed in tables 8 - 11. Modifications to Chiasson's results (based on data collected from the dissections) are indicated in the text. The tables are arranged in such a way that all muscles originating from a common element of the pelvic girdle are listed together for easy reference. The relationships between the muscles are also presented in diagrammatic form to illustrate successive stages in the dissection, in dorsal and ventral view (figs. 38a and b and 39a, b and c). The sites of origin and insertion on the pelvic girdle are indicated in fig. 40.

PECTORAL MUSCULATURE

Those muscles listed by Haughton (1864-68) and Chiasson (1962) as originating in the pectoral region were identified, and their sites of origin and insertion verified. Modifications to earlier work are indicated in the text and are based on the dissection results presented in this work. Their sites of origin and insertion are presented in tables 12 - 14 (after Chiasson 1962). These tables are arranged in such a way that all muscles originating from a common element of the pectoral girdle are listed together for easy reference.

The relationship between the pectoral muscles is presented in diagrammatic form (fig. 41a and b) showing dorsal and medial views. The arrangement of sites of origin on the pectoral girdle is also presented in diagrammatic form (see fig. 42). Chiasson does not include such a figure in his work (1962), although this is otherwise the most recent and comprehensive record of pectoral musculature in Alligator.

BIOMECHANICAL SITUATION IN FOSSIL CROCODILIANS

ORIGINAL DESCRIPTIONS

METHODS

Particular aspects of the osteology are re-examined below and on pp. 115 - 134.

Emphasis is placed on the osteological characters which discriminate between similar bones in the two Callovian genera and on comparisons of palaeontological and neontological material. The descriptions concentrate on:

a. the shapes of the bones (due to the diagenetic effects on the preserved material in the Oxford Clay, this is the line of evidence which supplies the most reliable information).

b. shapes of articulation surfaces.

c. the orientation of the articulation surfaces, in relation to the limb bone shafts.

Estimation of the effects of diagenetic compression is problematical, although it seems reasonable to assume these effects to have been approximately uniform throughout the very concentrated geographic area in which material was collected. No mention of this important aspect is recorded in previous descriptions. Andrews (1913 and 1915) appears to have disregarded the types of effects diagenisis could have on certain aspects of limb and girdle osteology as they appear in the fossil material. For example he draws attention to what he considers to be taxonomically significant characters (at species level) as follows:

"The tarsus differs in M. superciliosum from that of M. laeve, in having the constituent bones less flattened from above downwards, and with more strongly convex articular surfaces" (1913 p. 177).

(i) PECTORAL GIRDLE AND FORE LIMB, STENEOSAURUS

The upper portion of the scapula is expanded, with faint rugosities and striae suggesting the presence of a suprascapular cartilage extending the area during life. The proximal border is thickened with an oblique, ovoid facet positioned posteriorly and externally, forming the upper portion of the glenoid, and anteriorly a terminal triangular surface for fusion with the coracoid. Andrews' description (1913 p. 106) does not emphasise the character which discriminates between the form of the pectoral girdle in living crocodiles and Steneosaurus, namely the reduction in the acromion

process of the scapula (see pl. 27). The proximal portion of the coracoid shows only limited convexity (see pl. 27). Postero-externally an ovoid shaped facet forms the lower part of the glenoid.

Important aspects of the osteology of the humerus include the following: the shape of the articulating surface with the glenoid, which is oval, elongate and highly convex (cup like) (see pl. 28x). An asymetrical development of this surface is apparent in some bones (e.g. R3701 B.M.(N.H.), which show a greater development on the anterior side of the bone. There is a quite well developed delto-pectoral crest (see pl. 28y). The presence of pits and numerous tiny swellings suggests that there was cartilage around the head and along the dorsal border to the delto-pectoral crest (see pl. 28). The orientation of the articulation facets is particularly interesting, because the head shows a deflection towards the mid line of the body, while the distal condyles are deflected away from the body. These articulation surfaces remain parallel with each other. The humerus in specimen R2617 B.M.(N.H.) illustrates a variation from the form outlined above. The head is deflected inwards to a smaller degree and thus the articular surface is approximately at right angles to the shaft of the humerus, a greater angle than in the majority of specimens belonging to this genus, whose morphology corresponds closely to that illustrated in pl. 28c.

The olcaneon process is greatly expanded, although compressed. In the region of the olcaneon process are rugosities indicative of tendinous muscle attachment, and the dissection results indicate this to be a region for muscle attachment (see tables 12 - 14). The distal facets are at right angles to the long axis of the ulna. Details of their articulation with the carpals are not known.

COMPARISON WITH RECENT CROCODILES

Pectoral girdle

a. The scapular facet faces more posteriorly, and less ventrally, than in recent crocodilians (see pl. 29).

This configuration possibly allowed more dorso-ventral flexibility at the hinge joint. It is impossible to know to what extent these movements were restricted by ligaments crossing the joint capsule which leave no recognisable trace in the fossil.

b. The reduction in convexity of the proximal blade of the coracoid is compared with the form of this bone in recent crocodiles in pl.27. This feature, however, may be the result of diagenetic compression.

c. The morphology of the articulation facets comprising the glenoid are similar in the palaeontological and neontological material.

d. The gross morphology of the scapula and coracoid is similar in the fossil and recent material, and is illustrated in pl. 27.

Humerus

In recent crocodiles the head of the humerus is placed terminally and at right angles to the long axis of the shaft, approximately parallel to the distal condyles. These face posteriorly and articulate with the radius (inner condyle) and ulna (outer condyle). Thus the essential difference between these specimens and Steneosaurus is the position of the articulating surfaces with respect to the long axis of the bone. The deflection of the head slightly increases the distance between the delto-pectoral crest and the pectoral girdle in the steneosaurs.

Ulna

The olcaneon process is more expanded in Steneosaurus; the position and form of the articulation facets is similar to that seen in recent crocodiles, although compressed dorso-ventrally.

Radius

This appears closely similar to neontological material examined (see pl. 28b), although flattened as a result of diagenetic compression.

(ii) PECTORAL GIRDLE AND FORE LIMB, METRIORHYNCHUS

The scapula has a reduced shaft, with a small upper expension, but

this displays evidence of the presence of suprascapular cartilage, in the form of ridges, striae and swellings. This bone has a thickened proximal border which is expanded posteriorly to form a steeply inclined facet, comprising the upper half of the glenoid. A great reduction of the acromion process has occurred, and there is no evidence to suggest cartilaginous extension of the scapula in this region.

In R3016 B.M.(N.H.) the coracoid foramen (which pierces the anterior expansion of this bone (Andrews 1913 text. fig. 69A) has developed into a deep notch (see Andrews 1913 text. fig. 69B) (and here, pl. 29x). Posteriorly the dorsal border is thickened and developed into an oval facet, forming the lower part of the glenoid.

The humerus shows a reduced long axis with a terminally placed head, and articulating facet at right angles, therefore, to the long axis and parellel to the distal condyles (see pl. 28c). The shaft of the humerus is wide and there is no evidence for convexity of the articulating surfaces. The scapula shows a concave glenoid facet and the head of the humerus is convex. The retention of this morphological detail at this joint suggests that its absence at the elbow is a real feature, and not merely the result of post mortem crushing and flattening. This would seem to indicate a lack of flexibility across the joint separating the humerus from the radius and ulna. The shaft appears completely flat (see pl. 28c).

The disc-like radius and ulna are orientated in terms of pre and post-axial sides of the bones (Andrews 1913 and 1915). Their orientation with respect to one another and the humerus is problematical. If the accepted orientation of these two bones in relation to the humerus is correct (see Andrews 1913 text. fig. 70A) there must have been very well developed cartilage on the distal end of the humerus to facilitate attachment of the radius and ulna - otherwise their combined widths would exceed the available area presented by the distal articulation facets of the humerus (see pl. 30). This is in contrast with the situation in

the ichthyosaurs where we see an expanded distal region of the humerus (see pl. 31). There is evidence for cartilaginous attachment around the perimeter of both bones, which may have filled in the spaces between the points of articulation with the humerus and each other (see pl. 30).

Some detail of the phalange bones is recorded in Andrews (1915). These bones appear to retain their linearity, with some reduction in the convexity and concavity of their articulation surfaces.

COMPARISON BETWEEN METRIORHYNCHUS, STENEOSAURUS AND RECENT CROCODILES

Pectoral girdle

a. The reduction of the acromion process is most extreme in the metriorhynchids (see pl. 27).

b. A reduction in the bony area of the anterior part of the coracoid has occurred, as a consequence of the development of the coracoid notch. This is not evident in Steneosaurus or neontological specimens. There is no visible evidence to suggest that cartilage was attached around the borders of the notch.

c. The orientation of the scapular facet forming the upper part of the glenoid is similar to that in Steneosaurus (see p. 96).

d. The area of bone for muscle attachment in the pectoral girdle is reduced owing to the reduction of the acromion process and development of the coracoid notch.

Humerus

This is reduced in length. Its articulation facets are positioned at right angles to the long axis and are parellel to each other, with the head occupying the same plane as the distal condyles, i.e. no "twisting" of the humerus shaft - which contrasts the form of the neontological material seen in pl. 28c.

There is an increased distance between the head and delto-pectoral crest, in relation to total humerus length (see table 37) in comparison with Steneosaurus (see p. 86 and tables 12 - 14 for the mechanical significance of this feature).

Radius and Ulna

The morphology of these bones is in marked contrast to both Steneosaurus and recent crocodilians, as shown in pls. 30 and 28b.

(iii) PELVIC GIRDLE AND HIND LIMB, STENEOSAURUS

The ilium has a particularly well developed dorsal border, which is nearly horizontal with a prominent anterior angle. The ventral border is thickened anteriorly, and the development of two notches suggests the position of the articular surface for the proximal surface of the pubis, (see pl. 32 and fig. 43). Posteriorly the ventral part of the ilium forms the dorsal part of the acetabulum. The postero-dorsal portion of the ischium is expanded into a double sided facet; the inner part is an almost horizontal and slightly concave surface for fusion with the ilium, while the outer part is a concave, shallowly inclined surface forming the lower part of the acetabulum. (Caution must be employed with this type of evidence because the "contours" of the ischium may have been reduced during fossilisation and thus the depth of the acetabulum, being in part a function of this, would show a corresponding reduction). The anterior projection of the ischium has a facet positioned terminally, for fusion with the ventral border of the ilium. In the steneosaurs it appears that the pubes actually fused with the ventral border of the ilium. The resulting anterior extension of the ventral iliac border produces an increased area along the length of the anterior iliac border (see fig. 43 and pl. 32). Notching, swellings and striae suggest extensive cartilage around the dorsal part of the pubis and adjacent region of the ilium. The pubis is similar in morphology to that of recent specimens (see pl. 33A) with one oval terminally placed articulation surface.

The femur is sigmoidally curved and in general the form and the shape of the facets resembles that shown in living crocodiles (see pl. 34).

The general form and shape and orientation of the tibia and fibula are similar to the corresponding neontological specimens (see pl. 34).

The pes apparently consisted of five digits each comprising metacarpals and phalanges (the fifth digit is shown by Andrews (1913 p. 115 text. fig. 47A) as a residual digit). From the limited evidence available, it seems that the third digit was the longest.

COMPARISON WITH RECENT CROCODILES

Pelvic girdle

a. The anterior angle of the ilium is more strongly developed in Steneosaurus but there is a slight reduction in the postero-dorsal region.

b. The depth of the acetabulum is apparently greater in recent crocodilians. This is the result of the greater concavity of the ilium, and particularly the width and inclination of the ischium facet.

c. No facet exists on the underside and anterior part of the anterior projection of the ischium in Steneosaurus (for articulation with the pubis). This facet is clearly evident in recent specimens (see fig. 43).

Femur

A reduction of the fourth trochanter has occurred in Steneosaurus. This morphological detail is present as a rugose area.

(iv) PELVIC GIRDLE, METRIORHYNCHUS

The short dorsal border of the ilium is inclined at an obtuse angle from the short posterior iliac border . The long anterior and short posterior border combine to form the configuration shown in pl. 32B. There is a resultant loss of the dorsal-posterior area of the iliac blade (the "postero-superior corner" sensu Andrews 1913), (see pl. 32B) . The ventral border appears relatively smooth, and its posterior part in con-junction with the area of bone immediately dorsal to it, forms the upper part of the acetabulum, which appears shallow (although this could be the result of flattening of the ilium). The concentration of rugosities, pits and striae in the anterior half of the ventral border seem characteristic of the genus, and it is possible that these indicate fusion between the pubes and ventral iliac border. The ilium seems small in relation to the hind limb, with a weakly convex internal surface showing two poorly developed surfaces for union with the sacral ribs. The pubis

has a single oval facet, terminally placed (possibly associated with cartilage) for union with the anterior part of the ventral iliac border (see above). There is no evidence to suggest that it was in contact with the anterior process of the ischium. The characters of the surface of the outer distal region of the pubis (striae, grooves and swellings) suggest that it was covered with cartilage during life. The weak development of the anterior process of the ischium further suggests that it did not unite with the pubis, and there is no visible facet for such an articulation on either bone. The proximal posterior part of this bone bears a region for union with the posterior part of the ventral border of the ilium and a concave, shallowly inclined facet forms the lower part of the acetabulum.

COMPARISON BETWEEN METRIORHYNCHUS, STENEOSAURUS AND RECENT CROCODILES

Pelvic girdle

a. The orientation of the dorsal border of the ilium approaches a right angle in Steneosaurus and recent crocodiles, but is inclined at an obtuse angle from the posterior border in Metriorhynchus.

b. The dorso-posterior area of the ilium has been lost in Metriorhynchus.

c. The anterior notches on the ventral border of the ilium, which are characteristic of the corresponding area in Steneosaurus are absent in Metriorhynchus.

d. The surfaces on the ilium for union with the sacral ribs are weakly developed, when compared with Steneosaurus and recent crocodilians.

e. The ischia and pubes correspond closely in general morphology with Steneosaurus.

f. The shape and depth of the acetabulum is comparable with Steneosaurus but shallower than in recent crocodilians.

g. The reduced bony area of the pelvic girdle, and maintenance of a similar sized acetabulum, produces effectively an increase in the size of the acetabulum relative to the pelvic girdle in Metriorhynchus.

Femur

This is closely similar to that of the steneosaurs, which in turn resembles recent material, with an openly sigmoidal shaft. Many rugosities and striae are developed around the head and continue on the outer and most of the inner sides of the proximal quarter of the bone. They are indicative of tendinous muscle attachment. The form of the head corresponds to that seen in Steneosaurus.

Tibia and fibula

The general morphology of these bones is closely comparable to that of the corresponding bones in Steneosaurus. The important difference in this case is not related to shape, but the reduction in length of these bones, relative to the femur, when compared with Steneosaurus (see table 36).

Pes

This comprises metacarpal and phalange bones which seem to be similar in morphology to Steneosaurus, although there is an overall reduction in their size. The longest digit in this genus, however, seems to be the fourth.

HYDRODYNAMICS

The following section is designed as an introduction to some aspects of hydrodynamics which relate to details of marine specialisation examined in pp. 108 - 115.

The forces that act when a fluid moves relative to a body, or a body relative to a fluid, are partially dependent on the pattern of flow. This is similar around bodies of similar shape, if the Reynolds number is the same. Calculation of the Reynolds number involves consideration of the physical properties of the fluid, its density and viscosity. It is expressed as: $\rho\mu\, a/n$ where ρ and n are the density and viscosity of the fluid, μ its velocity relative to the body, and a is a

length (the size of a particular part of the body for instance). (Alexander 1968 p. 209). It is conventional to express the Reynolds number as $\mu a/v$, where $v = n/\rho$ (and is known as the kinematic viscosity of a particular fluid). Examples of the kinematic viscosity of a selection of fluids are given in Alexander 1968 p. 210, table 4. Thus the Reynolds number summarises the properties of the water one must consider, in an examination of marine specialisation in a particular group of animals and, in theory, the preferred body design.

The principal types of flow pattern are shown in fig. 44a (after Alexander & Goldspink p. 225). Flow patterns like A occur at Reynolds numbers below 1; as the Reynolds number rises above 1 a gradual change to patterns indicated in B occurs. This pattern is maintained until the Reynolds number reaches a critical value, when the flow pattern changes abruptly to the pattern illustrated in C.

The study of hydrodynamics will involve consideration of a complex interaction of the following factors: the shape, size and velocity of the animal and the properties of the fluid (i.e. water) through which it moves.

When a body is moving through a fluid, a force acts backwards on this body along the direction of motion, which is called drag. Drag can be quantified and calculated by the equation $D = \frac{1}{2}\rho u^2 AC_D$ where D = drag, ρ = the density of the fluid, u = velocity of the fluid relative to the body, A = a characteristic area (Alexander 1968 p. 215) and C_D = the drag coefficient, which depends on the shape of the body and the Reynolds number. This amount, therfore, varies according to the properties of the fluid, and the size, shape and speed of the body.

Drag coefficients and Reynolds numbers have been plotted for bodies of varying shapes in fig. 45 (after Alexander 1968 p. 216) which shows the differences in drag coefficient at moderate Reynolds numbers for varying body shapes. This emphasises the importance of considering the speed at

which the animal is moving, in relation to the body shape it displays when attempting an estimation of the extent to which this form is an adaptation to an aquatic environment. The kinks in this figure at Reynolds numbers of 10^6, are due to a change in the type of flow in the boundary layer (see fig. 44a) which changes from laminar to turbulent with the increase in Reynolds number above a "critical" value. At this point flow is laminar over the front part of the body and turbulent towards the rear (Alexander 1968).

The onset of turbulence increases friction drag (see below). There is a range of Reynolds numbers in which the drag coefficient of a streamlined body can be reduced by preventing all or part of the boundary layer from becoming turbulent (see Alexander 1968 p. 219). To reach its critical value, a body must be large or fast or both e.g. Dolphins, which are large animals and swim quickly and, therefore, have large Reynolds numbers. Fig. 45 indicates that shape affects drag values, a phenomenan that can be explained by considering drag in more detail.

Drag has two components, friction and pressure drag. Friction drag corresponds to work done against the viscosity of the fluid immediately in contact with the body. This fluid is carried along with the body, creating a decreasing velocity gradient in the boundary layer. The wake from a body travelling through water consists of water which has been given kinetic energy, which must come from work done in driving the body along, against friction drag. "The part of the drag accounted for in this way is called pressure drag"(Alexander 1968 p. 217). Thus most of the drag on bodies which leave very disturbed wakes is accounted for by pressure drag.

Roughness has little effect on drag unless the irregularities of the surface area are big enough to protrude from the boundary layer. Since this decreases in thickness as the Reynolds number increases, irregularities that are unimportant at low speeds may have marked effects on patterns of

flow around animals at higher ones. This concept has great relevance to the development of ornament of cranial bones in the metriorhynchids. This characteristic has been related to streamlining by some authors (e.g. Steel 1973), but the relevance or significance of ornament in this respect is dubious. We have to ascertain whether the configuration of bone was of sufficient magnitude to protrude from the boundary layer, because only then will it affect the patterns of flow around the animal and thus its streamlining.

The most "popular" term used in the literature in conjunction with marine specialisation is "streamlining" (usually without adequate explanation). A streamline is a curve, whose direction is everywhere the same as the direction of the flow of the fluid (Alexander 1968). Streamlined bodies are designed to leave as little disturbance as possible in their wake, a well streamlined body experiencing friction drag, but relatively little pressure drag. The drag on a well streamlined body depends on a ratio of length to maximum diameter, termed the fineness ratio (see fig. 44b, after Alexander 1968 p. 217). Drag, by definition, acts in the same direction as the velocity of the fluid relative to the body (Alexander 1968).

When a symmetrical body moves through water along its axis of symmetry, the hydrodynamic force acts directly backwards and is all drag. If a symmetrical body moves at an angle, or an asymmetrical body moves in most directions, the hydrodynamic force acts at an angle to the path and can be resolved into a component acting directly backwards, drag, and one at right angles to drag, known as lift (Alexander 1968). Structures designed to produce lift in water are called hydrofoils. Ideally they are streamlined so as to maximise lift and minimise pressure drag. Lift is due to fluid flowing faster over the upper surface of the hydrofoil than the lower, the faster fluid has a lower pressure than the slower, by Bernoulli's equation.

This relates the pressure of a fluid P, density ρ, and its velocity u, at different points along the same streamline as follows:
$u^2/2+gh+P/\rho = k$ (h = a constant if the fluid is flowing horizontally), proving that any increase in u, must result in a decrease in P. Thus it explains the generation of lift (see above) by decreasing the pressure of the fluid flowing above the hydrofoil and creating an upward force, the pressure difference, between the upper and lower surfaces of the hydrofoil. The amounts of lift depends on the angle of the hydrofoil relative to the water, known as the angle of attack (see fig. 44c, after Alexander 1968 p. 229).

The lift coefficient is defined by the equation $L=\frac{1}{2}u^2AC_L$ where L = lift, C_L = the coefficient, u = velocity and A relates to the shape/size of the hydrofoil (i.e. the area).

Any attempted interpretations of osteological modification occuring in fossils in terms of their acquisition of a hydrofoil, therefore, involves consideration of the shape of the limb achieved through modification of bone or soft tissue, the velocity at which it seems reasonable for this animal to move and the orientation of the limb and associated values of lift and drag.

Movement of a body through water may also be accomplished by rowing. This method of propulsion consists of power strokes, in which the oars move backwards relative to the body and drive volumes of fluid backwards, to create forward thrust, alternating with recovery strokes in which they move forwards again. During the recovery stroke, the drag must be reduced to a minimum (achieved for example in sea-lions by medial rotation of the limb (English 1977). The oars should be designed (i.e. through osteological or soft tissue modification) to give large drag values at low velocity. Fast rowing boats are streamlined, but their oars have large flat blades, which are held perpendicular to their path through the water to create as much drag as possible and, therefore, move maximum amounts of

fluid backwards. Similarly the amount of water accelerated during limb paddling is related to the surface area of contact between the limb and the water. The types of osteological and tissue modifications one might expect, in this instance, would include a decrease in the moment arm of resistance or an increase in the distance of relevant muscle insertions in relation to the joint (to increase the mechanical advantage of the muscles producing the thrust used in rowing), concomittent with a broadening of the limb of reduced length, to maximise surface area. Large values of thrust are produced most effectively by acceleration of large amounts of water to low velocities (Alexander 1968). Also one would expect the development of sufficient areas of bony attachment in the limb girdles for the volumes of muscles which provide the required muscular effort. All of the above increase the effectiveness with which a force is applied to the water via the limb.

CHARACTERISTICS CONSIDERED BY PREVIOUS AUTHORS TO BE SIGNIFICANT FOR AQUATIC LIFE FOR THE CALLOVIAN CROCODILES

Andrews (1913) made several observations regarding the osteological variations between the genera Steneosaurus and Metriorhynchus, in relation to marine specialisation.

"The crocodilia of the Oxford Clay were probably all aquatic to a much greater degree than the modern representatives of the order, but the various groups differ considerably among themselves as to the extent to which the skeleton has become modified for pelagic life" (p. ix). According to him, the Geosauridae represented in the Oxford Clay by various species of Metriorhynchus had undergone extreme modification for a purely aquatic life.

Fraas had previously (1902) described and discussed the various skeletal modifications of the family Metriorhynchidae (and their significance), with reference to the genera Geosaurus and Dacosaurus in particular.

In addition to these major works there are others in which reference to the "extreme modification" of the metriorhynchids for a purely aquatic life is made, and comparisons are drawn between this genus and Steneosaurus in terms of the degree of marine specialisation they show (e.g. Steel 1973 and Buffetaut & Thierry 1977).

Andrews (1913) referring in places to Fraas (1902), based his evidence for marine specialisation on the following characters possessed by the metriorhynchids: the head has a pointed snout: the prefrontals form a protective projection above the orbits: the neck is shortened: the fore limb is paddlelike and very small compared to the hind limb: the terminal section of the tail is deflected downwards and carries a fleshy fin: the dermal armour has been lost: sclerotic rings are present: there is the complete loss of ornament in some forms.

He followed the premise that one form equals one function and did not consider that form may reflect a mosaic of functional "compromises". His ideas have been reiterated uncritically by subsequent authors (see above).

Some of these observations should be re-examined critically to test if the "one form, one function" premise seems to be an accurate one, i.e. whether the accumulation of the characters that have until now been cited as the formula for successful exploitation of the marine environment by the metriorhynchids is the only, or most favourable, combination. It is important to do this because the Teleosauridae, represented here by the steneosaurs, are said (as recently as Buffetaut & Thierry 1977) to be much less specialised in this direction. This conclusion is based on the following observations (after Andrews 1913): the premaxillary region of the snout is expanded and not pointed as in the metriorhynchids: the prefrontals do not overhang the orbits: the neck is relatively longer: the fore limbs, though reduced in size, are not paddle like: the end of the tail is not deflected to form the support of a large terminal caudal fin: Andrews (1913) seemed to place particular emphasis on observations 3 and 4.

PREVIOUS STUDIES USING FOSSIL VERTEBRATES AND RECENT AQUATIC MAMMALS IN AN ATTEMPT TO ASSESS AQUATIC ADAPTATION

Ichthyosaurs

In these animals the main propulsive organ was the reversed heterocercal tail with a dorsal fin. The fore limbs of some ichthyosaurs were greatly developed, showing increased numbers of phalanges and digits (hyperphalangy and hyperdactyly). The hind limb was very reduced in size with vestigial pelvic girdle elements. A paddle-like shape was acquired in the fore limb through modification of the propodials i.e. the humeri, to approach a more equidimensional form, and similarly the radius and ulna (the epipodals) assumed this form. The carpals, metacarpals and phalanges were flattened and disc-like, fitting very closely as shown in pl.

Consideration of the proportions between the limb elements shows the propodals to be shortened, with corresponding elongation of the epipodals and metapodals through hyperphalangy.

Plesiosaurs

These reptiles appear to have swam by means of four large paddle-like limbs, although the presence of a dorsal fleshy fin on the comparitively small tail indicates (according to Halstead 1969), there to have been some role for this organ in locomotion. The modification of limb elements in these animals is similar to that described above for the ichthyosaurs. The propodals retain some traces of linnearity - their axes remaining greater than their width - where the degree of linnearity exceeds that seen in the ichthyosaurs. The long axis is further reduced in the epipodals, where the axis and width become more similar. The four "paddles" are similar in overall size. The proportions between the propodals, epipodals and metapodals contrasts the situation seen in most ichthyosaurs, the humeri are more elongate giving an improved mechanical

advantage (see p. 86) and thus a more powerful rowing stroke.

It is concluded by Johnson (1977) that some ichthyosaurs have fore limbs which are specialised in their proportions for speed of movement, and in their morphology as hydrofoils. The situation is rather more complex, however, in that individuals of some genera of ichthyosaurs, in which the pectoral elements are large and robust, seem to have possessed a greater mechanical advantage in the operation of the limb. This variation may be a reflection of the manner in which the limb was used in different ichthyosaurs (Johnson 1977).

The limbs of plesiosaurs appear to have been specialised for rowing, being the main propulsive organs of the animal, and fulfilling the functions of "oars" (see p.107).

The above observations indicate that in terms of "advanced marine specialisation" as depicted by the ichthyosaurs and plesiosaurs, one might expect to see a variety of osteological features combined in contrasting patterns which appear to have been "recipes" for success in the marine environment.

Two distinct lineages evolved from the fish eating plesiosaurs of the Trias and these are considered to have differed primarily in their dietary preferences (Halstead 1969). One group retained large numbers of simple,slender, sharply pointed teeth (upper and lower dentition acting as a fish trap), evolving a small head and a progressively longer neck; these are known as the elasmosaurs. The pliosaurs contrasted markedly with the morphology outlined above. Their teeth became massive, blunted and were not so closely adjacent in the jaws. These morphological modifications were coincident with progressive enlargement of the head and shortening of the neck. Halstead (1969) suggests that such dentition might be suitable for the predation of cephalopods. This dimorphism in skull morphology and dentition is very interesting, with respect to the variance in cranial features and dentition in the steneosaurs and

metriorhynchids (see pp. 60, 61 and 72), which may be in part the expression of morphological responses to different dietary influences.

The morphological requirement of a particular aquatic animal will depend on its speed of movement through the water as outlined in p. 104 (i.e. the "cruising speed" of that animal). This concept, namely that contrasting methods of locomotion, using different parts of the body, might occur at different speeds was never applied to the marine crocodiles. It has a fundamentally important significance i.e. that the steneosaurs might have functioned quite adequately at slower speeds in the water than the metriorhynchids (who possess more obvious osteological modifications). This is not synonymous with the apparently widespread conclusion that the former are far less aquatic than the latter, but only relates to their speed of movement.

The extensive range of morphological modifications displayed by living animals which are aquatic to varying degrees, suggests that we should not aim to define a single morphology to correlate with a function in a particular environment. Information documented in the literature about movement at different speeds in a selection of aquatic animals, can be applied to a hypothetical situation in which the two genera of Callovian crocodiles spent the majority of their time swimming at contrasted speeds.

The first observations relate to the living crocodilians:

"Crocodilia use the tail exclusively for speedy swimming, and the hind limbs to a considerable extent furing sluggish progression.... the alligator may "walk" slowly through the water with all four limbs, or may progress by means of the pedes alone, while during more rapid progression, the appendages are pressed to the body, while the tail is lashed from side to side" (Howell 1930 p. 22).

"If one watches an actively swimming alligator, he will observe that the front legs are folded or "collapsed" by the side of the body, while

the hind legs much bent are used only slightly in propulsion. The animal swims by sinuous movements, like that of a snake on land, extending throughout the tail and part of the body"(Williston 1914 p. 65). "The tail is much elongated and compressed, forming a powerful means of propulsion in swimming.... the limbs are of the ordinary elongated type.... and are not much use for propelling the body in the water; the front legs indeed are usually held close to the body while the animal is swimming" (Williston loc. cit. p. 196).

Observations on locomotory patterns in the river otter (Lutra canadensis), sea otter (Enhydra lutris) and the harp seal (Pagophilus groenlandicus) have been described and analysed in relation to the external morphology of these species (Tarasoff, Bisallon, Pierard & Whitt 1972). This study illustrates that various parts of the anatomy of these species acquire propulsive or balancing/steering functions at varying speeds, and that the organ that is supplying the primary source of propulsion may vary depending on the speed of motion. The authors show that in more highly specialised aquatic animals either the limbs or tail have developed into the principal propulsive organ (although the pattern does vary with the speed of motion). The more amphibious mammals often use two body regions for locomotion and in general each region, used alone, appears less efficient than the corresponding region of the more aquatic animals. Concomittant with greater aquatic adaptation, there is an increased tendency to restrict the area of aquatic propulsion to one body region. In the animals analysed in the above study, Lutra, Enhydra and Pagophilus, this anatomical modification takes the form of a progressive increase in the surface area of the foot coincident with its increasing importance as a means of aquatic propulsion, accompanied by a decrease in tail surface area in this order (indicating the decreasing importance of this region for aquatic propulsion).

As explained in the hydrodynamics section (p. 108), locomotor facility in an aquatic medium requires a large surface area, which can be used to

displace maximum volumes of water (i.e. large values of thrust are produced most effeciently if a large volume of water is accelerated to a low velocity).

The modification of limbs used in aquatic propulsion in mammals ranges from membraneous webs between the toes (e.g. ducks, seals and otters) to fore flippers of the sea-lion. These studies illustrate that otters swim quite adequately without apparent osteological modification of their limbs, and that it is the cartilage and skin which assume the paddle form in sea-lions with only a minimum of osteological modification (English 1977 p. 343).

Specimens of the estuarine crocodile, C. porosus, are documented in the literature (Guggisberg 1972) as able swimmers over extensive distances, although they show no osteological modifications of their limbs. C. porosus is known to have a proportionally longer tail than the other crocodile species (relative to trunk length) and the development of this character is attributed to the long distances travelled out to sea by this species (after Wermuth (1964) in Webb & Messel (1978).

Williston (1914) concluded from his studies of sea otters, beavers, sea-lions and whales, that their methods of adaptation varied, and he used these mammals to draw analogies with fossil reptiles.

The above examples serve to introduce a note of caution into functional interpretation. It is increasingly apparent that it is extremely difficult to determine the total degree of limb modification from skeletal evidence alone. In addition it will not be feasible to select one "limb and body plan" to the exclusion of all others which will perform a particular function with maximum efficiency. This seems particularly relevant in view of the far reaching implications about the mode of life of the steneosaurs and metriorhynchids, which have been based largely on the osteological differences between the forelimbs and tail in these crocodiles. There seems to have been little regard for limb, tail and body proportions, form of the soft tissue, or comparative studies with the

types of movement and associated morphology in living crocodilians and other aquatic animals. According to Cott (1961), the Nile Crocodile has perfect mastery of aquatic locomotion, although this species lacks any osteological modification of the kind seen in the metriorhynchids. This serves to emphasise the extent to which recent crocodilians can move effectively in an aquatic medium with the "apparatus" that they possess.

It is proposed that the osteological differences seen between Steneosaurus and Metriorhynchus might reflect the speeds at which these animals were most suited to swimming, rather than different degrees or levels of marine specialisation i.e. that different forms = equal adaptation.

THE EVALUATION OF THE PRECEDING CONCLUSIONS, IN THE LIGHT OF THE INFORMATION PRESENTED IN THIS CHAPTER

(i) SKULL CHARACTERS

Similarities in the morphology of this region in recent and extinct groups of crocodilia are seen by Iordansky (1973) and Langston (1973) as largely due to the convergence in mode of feeding, and Langston cites the following examples: Teleosaurus (Jurassic) and Dryosaurus (Cretaceous), two mesosuchians, and Gavialis (Cenozoic) and Thoracosaurus (Upper Cretaceous) eusuchians, showing parellelism in the development of fish catching adaptations.

He also illustrates the superficial resemblance between the arrangement of the dorsal cranial bones in Metriorhynchus and the mosasaurs, i.e. the broadening of the rostrum particularly in the frontal region, and modification of the cranium and rostrum pattern (fig. 3 p. 269 Langston 1973). These characters displayed in the mosasaurs are widely accepted as an attempt by the animal to reduce turbulence around the skull and introduce an additional factor i.e. streamlining which seems also to

influence cranial morphology in the metriorhynchids. It will be superimposed on characters associated with feeding (i.e. the jaw mechanics and muscle attachment outlined in pp. 87 -93).

a. Palate

Langston (1973) interprets this character in terms of structural mechanics. Extreme lengthening of the rostrum induces increased stresses to act upon this region. Bending movements in the region immediately anterior to the orbits makes the skull extremely vulnerable to fracture here. Expansion and union medially of the palatal bones, in Langston's opinion, counteract these stresses, building a strong tubular construction, where the most posterior of the palatal bones, the palatines, are fused with the pterygoids which are fused to the brain case resulting in a rigid suspension.

b. Loss of contact of nasal and premaxillary bones

There is an interesting correlation between the gavials, metriorhynchids and steneosaurs (particularly the latter). The nasal bones in the majority of the former, and all specimens belonging to the latter genus, have lost contact with the premaxillae as a result of increased anterior elongation of the maxillary bones. Langston (1973) believes that this further perfects the tubular design of an elongate snout, reducing by half the number of longitudinal zones of weakness (i.e. the sutures).

c. Undulations of the jaw margins

The biological significance of this character appears to be that it permits the crocodiles to hold their particular type of prey (i.e. small mammals) more firmly between the jaws. This explanation would seem to be supported by the absence of the character in fish eating gharials and the Callovian crocodiles, Steneosaurus and Metriorhynchus. Its absence, however, in the broad-skulled metriorhynchids and the more robust steneosaurs is fascinating. It seems to reflect an absence of the size and kind of prey in the Callovian environments for which the acquisition of the

undulations by the predator would be an advantage. The development of a broad snout, and in the large steneosaurs, blunted tooth crowns, would seem to indicate some kind of dietary influence. A broad snout will increase the resistance of the water to rapid closure of the jaws on the prey.

d. Size of the supratemporal fenestrae

In living crocodilians the relative snout length and form can be correlated with the development of the supratemporal fenestrae, the dimensions of which depend on the bulk of the M. adductor externus profundus. The relationship is explained fully on p. 90 .

The situation is somewhat more complicated in the Callovian crocodiles. The broad-skulled crocodiles retain the extremely large supratemporal fenestrae (which contrasts the situation in recent crocodiles). Some of the Callovian specimens with long and slender jaws actually have relatively smaller supratemporal fenestrae. It seems that the correlation between jaw form, mode of feeding and, therefore, the development of the various jaw adductors in the Callovian specimens is the consequence of the food available in the marine environment, which contrasts with that existing in river habitats. Here, recent specimens with long jaws feed mainly or exclusively on fish (e.g. the gharials), and those with jaws of moderate length feed on various animals in addition to fish, including reptiles, birds and mammals. In the Oxford Clay environment it is possible that the broader snouted forms fed largely on shell food, from the prolific invertebrate faunas of the Oxford Clay (Duff 1975). These include molluscs, ammonites, crustaceans and belemnites. Predation on this type of prey might have removed the need for morphological features to facilitate the capture of small, agile fish (and, therefore, rapid jaw closure would have become less important). This explains the feasibility of a very broad snout, but does not explain the retention of large supratemporal fenestrae, (as it is the M. adductor externus profundus which produces the rapid jaw closure).

The explanation might be related to the fact that the above muscle is advantageous at small angles of jaw abduction. Shell food would be small relative to the crocodilian jaws and, therefore, one would expect only minimal development of the M. pterygoideus anterior because there is nothing for the broad-skulled crocodiles to have to rip, seize or manipulate at large angles of jaw abduction (see p. 90). Small angles of jaw abduction are also supported by the minimal development of the pterygoid bones (see below). It seems that the M. adductor externus profundus was the most important jaw adductor for the Callovian specimens of both genera, in spite of their contrasting jaw forms.

Predation on the type of fauna outlined above would also explain the absence of undulations of the jaw margins in the broad-skulled crocodiles (see p. 92).

e. Pterygoid "wing" or flange development

The functions of these bones were outlined on pp. 92 - 93. Their minimal development in both Callovian genera would appear to support Iordansky's hypothesis (1973) that they prevent medial displacement of the mandibular rami. Thus the degree of development in the Callovian crocodiles would be sufficient to prevent displacement of the mandible at narrow gapes. It should be noted that poor preservation of the palate in many of the Callovian specimens limits the available evidence. (The poor preservation results from severe dorso-ventral flattening and the resultant crushing of bones constituting the palate).

f. Premaxillary development

Irregularities in the margin of the snout and jaws are known in "shorter-snouted recent crocodiles" and are described on p. 92. These exceed the premaxillary expansion seen in the steneosaurs, in terms of magnitude of contouring of the jaw margins. The presence of undulations does not appear to affect the swimming ability of the recent crocodiles which display them.

The effect of the premaxillary expansion on the hydrodynamism of the skull seems to have been overemphasised. It is possible that its presence gives some indication of the slower speeds at which the steneosaurs commonly swam, being likely to affect the amounts of drag and turbulence induced by swimming at speed, but no indication of actual ability to function efficiently in an aquatic environment.

g. Prefrontal bones

The development of these bones in Metriorhynchus is thought to be analogous to the osteodermal eyelids of recent crocodilians (Langston 1973). Some authors have suggested their function to be a protective one, shielding the eyes from the water during sudden lateral movements of the head while swimming rapidly through the water (e.g. Williston 1914).

h. Tooth form

Teeth are essentially homodont throughout the range of skull forms. In some of the larger steneosaurs there is some variation in crown bluntness irrespective of the position of the tooth in the jaw. Some recent crocodilians (e.g. C. niloticus) have blunter teeth which are restricted to the posterior regions of the jaw. The teeth are conical with slight backward and inward curves in the Callovian genera. The enamel is raised into fine longitudinal ridges. Unlike those of the Alligator, there is no "waist" at the level of emergence of the tooth from the gum in the Callovian crocodiles. Coupled with the lack of jaw undulations and retention of large supratemporal fenestrae, this may be another reflection of their small prey (as compared with the alligator's prey for instance, which can include cows and humans).

i. Sclerotic plates

Well ossified sclerotic plates are only recorded in one genus of the Callovian crocodiles; the metriorhynchids. Their biological role appears to have been to strengthen the sclerotic coat of the eye ball by a bony skeletal structure, and is convergent with non crocodilian aquatic reptiles (e.g. Ichthyosaurus).

j. Number of cervical vertebrae

Although it is true to say that there are two more cervical vertebrae in the steneosaurs (when compared with the metriorhynchids), the total number of vertebrae in the former does not exceed seven. Thus the length of the neck in the steneosaurs remains shorter than in recent crocodiles (amphibious), where nine cervical vertebrae are present (see table 34 suppl.)

(ii) FORE LIMB, METRIORHYNCHUS

In this genus, osteological modification has apparently coincided with a reduction in size of the limb, pectoral girdle and hence, it is presumed, associated musculature.

The mechanical advantage of the limb is increased in relation to its size because the position of the deltopectoral crest has altered (as shown in table 37). The muscles which insert on this crest have been investigated by dissection, and are listed in tables 12 and 13. This could reflect the fact that these muscles are now responsible for moving the limb as a whole. The mobility between elements is questionable in view of the apparent reduction in joint and articulation surfaces, the disparity in size between the distal end of the humerus and the width of the radius and ulna, and the lack of evidence for extensors and flexors within the limb. The osteology would appear to suggest that the limb elements were embedded in cartilage and were, therefore, largely immovable. Apparently the pectoral muscles used their increased mechanical advantage to move these limb elements as an entity. Flexibility within the fore-limb might increase the possibility of collapse (at the elbow) under water pressure at high speeds. Retention of shape at speed is essential if the hydrodynamism of the limb is to be maintained (being in part a consequence of the shape of the limb, see pp. 104 and 107).

Andrews (1915), ventured the opinion that "the limb had already become so small that it can have been of little use in swimming or even balancing" (p. 447) and yet had previously commented "the paddle of

Metriorhynchus as compared with that of Geosaurus does not seem to have undergone such extreme modification, especially in its proximal region (1915 pp. 446 and 447). Reference to (Fraas 1902 pl. 8 fig. 3) confirms the extent of the morphological modification and reduction in size of the geosaur limb, indicating that the appearance of the metriorhynchid limb was only part of a progressive evolution in limb form. This suggests that the osteological modification is being actively selected and this does not seem to be compatible with Andrews' theory of uselessness.

"It is virtually impossible to prove that a particular structure has no function at all and while size and shape are suggestive they can be misleading" (Johnson 1977 p. 219).

Consideration of the size and apparent strength of the forelimb in Metriorhynchus, suggests that it may have been used for orientation as a hydrofoil. The change in osteology reflects an attempt to create a hydrofoil (which to be effective should be streamlined). Progressive skeletal change to this end can be monitored between the metriorhynchids and geosaurs. Such a function might require less muscular effort than a rowing action for instance.

The shapes of the socket at the glenoid and the shape of the articular surface at the head of the humerus indicate that a large arc of movement would be permitted by the elongate, convex head in the glenoid before the limb would "slip off" the condyles i.e. become disarticulated. Some dorso-ventral movement seems feasible, but it is not possible to determine the plane of movement of the forelimb i.e. to distinguish between horizontal and other planes of movement from the skeletal evidence alone. Little evidence for medial rotation of the limb is apparent, but the sphericity of the articular surface of the humerus has probably suffered distortion of its dimensions during fossilisation.

The reduction in the acromion process apparently signifies the differential development between dorsal and ventral muscles originating

in this region, i.e. the M. deltoides scapulae and the M. supracoracoideus respectively (see fig. 42). Apparently protraction is now effected without the assistance of the former muscle, or perhaps these animals had less ability to protract the limb, and more subtle changes in the orientation of the limb sufficed. This would seem to preclude a rowing action for the limbs. Development of a deep coracoid notch in some specimens might also indicate a reduction in the M. supracoracoideus and suggests further the decreased relevance of limb protraction in some of the metriorhynchids. In addition, there is no weight support function of the muscles originating in this region in an aquatic animal.

(iii) FORE LIMB STENEOSAURUS

In this genus a reduction in size but lack of osteological modification of the limb has occurred. The backward deflection of the humerus head, in conjunction with the position of the articular surface, results in a relative increase (although small) in the distance between the delto-pectoral crest and pectoral girdle to that seen in recent crocodiles, i.e. an increased distance between the origin of muscles on the proximal portions of the scapula and coracoid and their insertion on the proximal portions of the humerus (running across the expanded proximal region). This increased volume (length) of muscle, in conjunction with the retention of a large coracoid might reflect that it was difficult (because of water pressure), but important, to be able to move the limb forwards (the M. supracoracoideus originating in this region, see table 13), thus requiring a small increase in mechanical advantage of the limb.

A hinge joint existed at the glenoid and although a wide arc of movement appears possible, it is not possible to determine with any certainty the plane of movement about the hinge joint.

The delto-pectoral crest is not raised in Steneosaurus in contrast to recent specimens. This seems to reflect the lack of the weight support function of the fore limb which, in recent crocodiles, is effected by muscles running from the pectoral girdle to the delto-pectoral crest.

There is an apparent retention of mobility within the limb bones, reflected in the development of articular surfaces on the humerus, radius and ulna. There is a smaller distance from the glenoid to the delto-pectoral crest in this genus when compared with Metriorhynchus (see table 37). This seems to correlate with the retention of mobility of the limb bones and corresponding development of extensors and flexors. We can see some strong evidence in support of the development of extensors. The expansion of the olcaneon process of the ulna (posterior margin) and the long axis of the distal condyles of the humerus strongly suggest that the limb retained the ability to be flexed and extended, using the powerful extensor (M. anconeus) which inserts in this region (see table 12 - 14), in conjunction with the M. coracoantibrachialis and M. humero-antibrachialis (flexors). The retention of flexibility within the limb might indicate its use during periods of emergence and movemenţt (albeit limited) on land, during breeding periods for example. Movement seems to have been effected in the sprawling posture, although stride length and thus efficiency of the movement would have been inhibited by the lack of lateral flexibility in the vertebral column (trunk), as indicated by the inclination of the zygapopheses (see p. 131).

Previous workers have been seemingly preoccupied with the lack of osteological modification of the limb bones in the steneosaurs, without regard for the reduction in size of the limb (see table 34 suppl.). Interpretation of this lack of modification should proceed with caution. The size factor will tend to restrict the possible uses of the limb more severely than its shape, which may have been extensively modified in the living animal by soft tissue (e.g. there is minimal skeletal modification in the sea-lion forelimb and it is the soft tissue which assumes the form of a paddle (English 1977). Such tissue will leave no trace in the fossil, (with the possible exception of skin outlines e.g. Liassic ichthyosaurs). It is difficult, however, to add significantly (in terms of material that

could sustain a weight support function) to the size of the limb. The relationships between the size of the fore and hind limb, which define the attitude and inclination of the body in any movement on land would, therefore, seem highly significant, and yet have never previously been considered. Cartilagenous extensions, amounting to up to one third of the limb length, are known in ichthyosaurs (Johnson 1979 pers. comm.) This tissue, however, could not have sustained the weight of crocodiles on land. These relationships are summarised in table and clearly indicate that Buffetaut & Thierry's (1977) picture of Steneosaurus "walking" across coastal beaches is somewhat idealised and unrealistic.

The reduction of the acromion process would apparently signify the reduced development of the M. deltoides scapularis (a limb protracter), (see fig. 42). The retention of a well developed M. supracoracoideus (see fig. 42) suggested by the development of the proximal blade of the coracoid, may indicate that protraction of the limb was effected without the assistance of the former muscle. It is difficult to reconcile the apparent increase in the volume of the M. supracoracoideus with a coincident decrease in the development of the M. deltoides scapularis when both muscles share a common function (Chiasson 1962) i.e. they protract the limb. Thus, the sum effect of the above developments would seem to be to cancel each other. It is difficult to envisage the advantage of transferring the function of a dorsal and ventral muscle pair, to a single and possibly enlarged ventral muscle.

(iv) HIND LIMB

The hind limbs of the Metriorhynchus and Steneosaurus do not differ to any great extent in the form, shape of articulation surfaces and orientation of the femur, tibia and fibula, or in relative size from each other or recent crocodilians.

The structure is essentially a "leg" and not a "paddle", and no marked

reduction of the limb has occurred, although some differences in the relationships (i.e. proportions) between limb elements are evident at generic level (see table 36). In all cases the fourth trochanter is reduced. Thus the general form of the propodals and epipodals is elongate, the femur being the largest of the limb bones, while the proportions of the tibia and fibula to the femur show some variation (see table 36). The tarsus in Metriorhynchus consists of four elements; the astragulus and calcaneum in the proximal row, and two distal and poorly known bones "probably representing the fused first and third, and fourth and fifth tarsalia respectively" (Andrews 1913 p. 176).

In the steneosaurs the tarsal bones consist of the astragulus, calcaneum and a distal bone the cuboid, the form and arrangement of which is seen in Andrews (1913) p. 115, text. fig. 47A, B and C.

Orientation

M^{c}Leod (1977 pers. comm.) has made the only reference to the reconstruction of the leg bones made by Fraas (1902) and Andrews (1913) although they are unique for crocodilians. The tibia and fibula are shown parellel to each other by both of these authors and in the same plane as the femur when it is lying on its side, the "dorsal" view of Andrews. Hence the crus and pes are rotated 90^{o} counter-clockwise from the position they occupy in the recent crocodilians, and the proximal end of the fibula lies alongside that of the tibia, rather than behind it. In this orientation the foot would project from the body in a horizontal plane. It appears that the only evidence Andrews and Fraas used in support of such a reconstruction is as follows:

a. The distal end of the femur is too narrow in its dorsal - ventral axis to articulate with the tibia and fibula in the position known in recent crocodilians.

b. Some specimens showed a position similar to their reconstruction prior to their excavation from the matrix.

Both of these facts can be accounted for by the post depositional effects encountered during diagenesis of the clay which forms the matrix.

M^{c}Leod (1977) reconstructed a hind limb of a metriorhynchid specimen as shown here in pl. 34 . The author would support this reconstruction in the light of research carried out during this study. In the context of this reconstruction it is interesting to re-examine the bones of the tarsus.

According to Charig (1972 p. 145 fig. 9) the foot of the "sprawler" is designed to act as a flexible base for the leg, and has an unspecialised tarsus. In recent crocodiles the calcaneum is locked to the metatarsus and extended as the tuber calcis, on which ankle and foot extensors and flexors are inserted (rather than on the metatarsus itself, so providing more leverage for these muscles without undue elongation of the tarsus). Most of the movement takes place at a ball and socket articulation between the astragulus and calcaneum (the former acting as part of the crus and the latter as part of the pes).

Fraas (1902) and Andrews (1913) show these bones as reduced flattened plates, with the tuber calcis orientated as shown in Fraas (1902 pl. 8 fig. 9). In combination with the presently accepted limb reconstruction, this would seriously inhibit movement between the foot, and ankle and leg, because the joint between the astragulus and calcaneum is the point of articulation through which most of the transmission of force from the foot to the limb occurs. The foot acts as the propulsive lever, where the weight of the limb acts against the ground, when on land, and against the water while swimming. Evidence which disproves the reconstruction of a flattened tarsus (Fraas (1902) and Andrews (1913), is provided by an astragulus and calcaneum (uncatalogued) in the H.M.(U.G.). Attention is drawn to these bones by M^{c}Leod (1977), who notes that they are not completely flat, but show a weak but definite ball and socket articulation. This evidence is supported by the tarsus of R3701 B.M.(N.H.) and M.B.

specimen (see pl. 35). Thus the flattening depicted in the reconstructions of Fraas and Andrews, is shown to be the result of post depositional effects and not evolutionary osteological change.

The revised orientation of the hind limb and osteological detail of the tarsus suggests some use of this limb against resistance provided by the water or possibly the ground (during periods of emergence for breeding and nest digging) which apparently necessitated the retention of flexibility and leverage in the ankle region.

(v) PELVIC GIRDLE

Consideration of the osteology of the pelvic girdle in Steneosaurus, recent crocodilians and Metriorhynchus has shown a progressive reduction in the dorsal region of the ilium (see pl. 32B) i.e. the dorsal border and dorsal part of the iliac blade. The osteology of the girdle is, at least in part, a reflection of the degree of development of muscles originating and inserting there.

The dissection results presented in table 10 outline the muscles which originate from the dorsal region of the ilium. A reduction in the dorso-posterior region of the ilium in the metriorhynchids has a dual effect:

a. Those muscles shown by dissection to originate in this region are apparently more weakly developed, or possibly absent, i.e. M. extensor ilio-tibialis, posterior, and possibly middle head, the M. ilio-fibularis, M. flexor tibialis externus and M. flexor tibialis internus (second head). This may correlate with the reduction in length of the epipodals seen in this genus, as their common function involves flexing and extending the shank and foot (Chiasson 1962). (It is also possible that these muscles may have originated instead from the increased area of the down-curved sacral ribs).

b. The area of the acetabulum is increased relative to the bony area of the girdle.

The decreased ability to flex and extend the shank, does not seem

compatible with the retention of a "leg" (when extreme modification of the fore limb had already occurred) i.e. why was this limb plan retained if there was a coincident decrease (through the reduction in the development of certain muscles) in the ability to manoeuvre it?

In the steneosaurs, there is an increase in the antero-dorsal region of the ilium, and this is the site of origin, in the specimens dissected, for the M. extensor ilio-tibialis anterior and middle head. This situation is possibly indicative of an increased ability to abduct the thigh against water pressure (during braking for example) or that this action was a difficult one to perform against the water pressure requiring development of correspondingly strong muscles. There is a very slight reduction in the posterior dorsal corner of the ilium in this genus, when compared with recent specimens, which might reflect a slight decrease in the development of shank flexors and extensors, although to a far smaller extent than in the metriorhynchids.

The arrangement of the sites of origin of the muscles on the ventral elements of the pelvic girdle as depicted by Romer (1923) and described by Chiasson (1962) have been verified by dissection. The development of these bones in Steneosaurus and Metriorhynchus is closely similar to each other and, in turn, to recent crocodilians (see pl. 33). Slight differences in their osteological detail are outlined in pp.100 -102. One cannot automatically presume, however, the development of ventral musculature to have therefore been similar. There may be other constraints on the osteology of the pelvis, in addition to the provision of sites for muscle attachment (e.g. that it must be of sufficient size to permit egg laying).

In addition to providing areas of origin for muscles, the ilium attaches the girdle to the vertebral column, by union with the sacral vertebrae (ribs). The strength of this attachment is reduced in Metriorhynchus (with respect to recent crocodiles and, marginly with

respect to Steneosaurus), with a coincident reduction in the area of rugosities developed where the sacral ribs fuse with the inner dorsal iliac surface. The sacral ribs show a progressive down-curving in Steneosaurus and Metriorhynchus when compared with the recent crocodiles (see pl. 36). This will affect the level of the acetabulum with respect to the level of the trunk. The area of the acetabulum, in relation to the bony area of the girdle is greater in Metriorhynchus than in Steneosaurus and, in both cases, the size of the acetabulum is large in relation to the femur head. This appears to reflect a large degree of flexibility at this joint. The depth of the acetabulum, as reflected by the outer ventral surface of the ilium, gives some indication of the range of positions at which the head of the femur could have been held and thus the angle of the limb, which is a consequence of the degree of adduction of the limb.

The ischium, in both genera, shows a slight increase in the development of the ventral blade anteriorly (see pl. 33B). The ischia appear to have joined at a more shallow angle than in recent crocodilians. They are less concave than their counterparts in recent specimens, and have a longer symphysial area. The degree of concavity of the distal portion of the ischium will affect its angle of inclination (the gradient). As shown by the dissection results in tables 8 - 10, the ischium provides the origin for the limb retractors.

There is evidence to support a comparable angle of inclination for the pubis (shown, by dissection, to provide the origin for the limb protractors).

The relationship between the position of these muscles and the fulcrum (i.e. the acetabulum) determines how much of the force applied by the above muscles can be resolved into a component which adducts the femur (see Charig 1972).

In the marine crocodiles, we see the progressive lowering of the

acetabulum by increasing the downward curvature of the sacral ribs, accompanied by possible shallowing of the angle of inclination of the ventral elements of the girdle. This configuration brings the sites of origin and insertion of muscles and the fulcrum closer to the horizontal plane, with a consequent decrease in the power of adduction.

Lowering of the acetabulum may also assist in the streamlining of the body (which would be particularly important in the metriorhynchids, where the angle of down-curving reaches a maximum) by lowering the "hips" (possibly in conjunction with widening of the shoulders by shallow inclination of the coracoids, although this is purely speculative).

During periods of emergence for nest building and egg laying, these animals would benefit from placing their acetabulum as close to the ground as possible i.e. low down on the trunk. Thus they would minimise the length of hind limb that must be retained to permit adequate "pushing power" during sprawling. Retention of an elongate hind limb in aquatic animals propelling with the tail poses obvious problems such as production of turbulence in the propulsive region, which may necessitate the limbs being held flush to the trunk when swimming, (see pp. 112 and 113). In the metriorhynchids this may be one reason why the caudal fin is placed around the 25th caudal vertebrae so that it is clear of any turbulence created in the region of the hind limbs.

The position of the acetabulum in recent crocodiles is a function of at least two factors, that a sufficient height is needed for leverage and adduction of the hind limb of suitable length to raise the trunk; also that the median thrust created in the adduction of the limb, and its thrust against the ground during a stride is directed into and absorbed by, the centrum of the sacral vertebrae. In marine crocodiles these forces will not be generated and, hence, the position of the acetabulum can be lowered beneath the level of the centra of the sacral vertebrae.

(vi) VERTEBRAL COLUMN AND TAIL

Krebs (1962) indicated that the orientation of the facets of the zygapopheses in the Metriorhynchidae and Teleosauridae would greatly restrict the degree of lateral movement within the column (see fig. 46 after Krebs 1962). This illustrates the orientation of facets in Alligator mississippiensis, and compares them with Steneosaurus and Balania (Cetacea). Flat horizontally opposed zygapophysial surfaces are known to permit relatively free lateral movement within the vertebral column, but restrict vertical flexure. An increasing tilt of these surfaces restricts lateral bending but allows greater vertical movement (Romer 1956).

Fig. 46 shows that there are many similarities between the vertebrae of Steneosaurus and Alligator, but that the articular surfaces of the zygapopheses are inclined very much more steeply in the former. Such an orientation would restrict sideways movement of the vertebral column, and thus lateral undulation of the body. Recent crocodiles still retain a degree of the piscine mode of undulation of the body during slow forward progression on land, which maximises stride length. This suggests that the Callovian Crocodiles did not frequent the land (the orientation of the zygapopheses in Metriorhynchus is comparable to Steneosaurus), where they would have been inefficient movers, owing to restricted stride length, which is a consequence of the limited lateral flexibility of the vertebral column.

It seems most feasible to suggest the body and anterior tail section were held rigidly whilst swimming, the propulsive force issuing from the tail. The orientation of the trunk and anterior tail zygapopheses might be an attempt to reduce the lateral flexes in the body, carried forward necessarily (and taken up) from tail vertebrae which would be flexed laterally to create the propulsive stroke. Lateral flexes in the body would be inefficient in the marine environment (in terms of the method of

propulsion used by the Callovian Crocodiles) and in this sense the "flexibility gradient" (see below) would act in reverse.

The posterior portion of the tail retains a greater degree of flexibility in the steneosaurs by a slight but progressive reduction in the development of the zygapopheses i.e. there is a "flexibility gradient" created by this modification of the size of the facets of articulation of the zygapopheses (see fig. 38 p. 101, Andrews 1913). The situation in the metriorhynchids is not as clear (because of the nature of the preservation of the material) but the acquisition of a reversed hetero-cercal tail appears to coincide with a similar development of the "flexibility gradient". The inclination of the zygapopheses would have allowed a large degree of dorso-ventral flexibility, possibly indicating the ability of the steneosaurs and metriorhynchids to dive, returning to the surface waters to breathe. If so, it is interesting that both genera appear to have equal ability to dive, in view of the fact that the metriorhynchids have, until now, been considered to be far more aquatically modified in their anatomy than the steneosaurs, e.g.

"The Teleosauridae preferred very shallow or temporarily emerged places, where they could move around thanks to their limbs which were still capable of walking on land" (Buffetaut & Thierry 1977 p. 151). It appears that these authors have disregarded evidence presented in the vertebral column and proportions of the fore and hind limbs and have paid too much attention to the contrasting morphology of Metriorhynchus and Steneosaurus, i.e. the fact that the fore limb in the latter genus has not been modified towards a paddle-like structure. The feasibility of either genus moving as a "sprawler" would involve a series of piscine undulations and this has been examined above. To be able to move on land by the high walk or gallop (Neill 1971, Zug 1974 and Singh & Bustard 1976) the fore and hind limbs need to be largely similar in overall length. The degree of size asymmetry in recent crocodilians is greatly reduced from the situation in

the Callovian Crocodiles (see tables 34 and suppl., 35 and 36).

Thus, although the fore limb is not structurally modified in the steneosaurs to the extent seen in the metriorhynchids, the difference in overall length between the fore and hind limbs, and the inclination of the zygapopheses in the former genus, would make progress on land by the above methods extremely difficult.

The usefulness of the tail as a propulsive organ is enhanced in the metriorhynchids by the acquisition of a caudal fin, indicated in the fossils by a tail flexure. This downward flexure occurs approximately at the 25th caudal vertebra, whose neural spine is directed vertically, while those of the vertebrae in front are directed backwards, and those situated more posteriorly,forwards. The latter are thickened, as seen in pl. 38 and, probably in conjunction with cartilagenous processes, would have strengthened a dorsal tail lobe. This pattern of vertebrae is known to have supported a fleshy caudal fin, because Geosaurus gracilis figured by Andrews (1913, frontpiece), in which the skin impression is preserved, shows a similar development of enlarged neural spines in the caudal vertebrae. The metriorhynchid tail also compares closely with the caudal vertebrae in ichthyosaurs which are known to support a dorsal tail fin because skin outlines of these fins are relatively common. Owing to the nature of preservation of material in the Oxford Clay, skin outlines of the fin in the metriorhynchids are unknown.

The ventral side of the tail in both genera of Callovian Crocodiles was strengthened by chevron bones. The anterior chevrons have long ventral processes which become progressively reduced as one moves posteriorly, to Y and then V shapes. No complete series has been preserved for Steneosaurus or Metriorhynchus but it seems reasonable to assume the arrangement in the latter to have been similar to that seen in Geosaurus (see Fraas 1902). In Metriorhynchus the ventral part of the chevrons is enlarged and laterally compressed behind the tail flexure, with facets

placed anteriorly and posteriorly (see R2054 B.M.(N.H.). If, as Andrews (1913) suggests, (and as is found in Geosaurus), these chevrons formed a closed series, the region would have been greatly strengthened. The combination of chevrons and enlarged neural spines would have restricted dorso-ventral flexibility of the caudal fin, which tells us something about the form of propulsive force issuing from here i.e. that it may have been in the form of lateral pulses of the tail, contrasting the direction of movement permitted in the other parts of the vertebral column. The presence or absence of the tail flexure has been one of the major factors considered in the ecological reconstructions and niche partitioning drawn between the steneosaurs and metriorhynchids. In both cases it is in the posterior region of the tail (and behind the flexure in the metriorhynchids) that the arrangement of the zygapopheses would permit the greatest degree of lateral flexibility. This suggests it to be the region from which the main propulsive force issued, by a scull like movement of the posterior section of the tail.

The tail in C. porosus does not have a fin, but these crocodiles are documented as swimming for long distances using this as the propulsive organ (Neill 1971 and Guggisberg 1972). This is important to bear in mind when considering the swimming ability of the steneosaurs.

Swimming and diving by animals of up to five metres in length (the maximum recorded size of a Callovian Steneosaurus specimen, which exceeds the maximum recorded length of any Callovian Metriorhynchus specimens analysed in this work) would "probably call for wide expanses of water. Thus the environment of the steneosaurs seems to have been the open seas" (Krebs 1962 p. 26). Krebs also notes in support of his theory that the remains of the steneosaurs are frequently found in juxtaposition in the sediment with those of the metriorhynchids.

SUMMARY

The disparity between the niches inhabited by the two genera of Callovian marine crocodiles (indicated by their contrasted morphologies and analysed in this chapter) would seem to have been previously exaggerated.

Evidence for the inhabitation of a "near shore" or coastal marine environment by the steneosaurs has been based mainly on the retention of a fore limb without modification to a paddle shape and the absence of a reversed heterocercal tail.

Evidence presented in favour of the metriorhynchids occupying more "open" marine environments was based on the acquisition, by this genus, of the following characters: a reversed heterocercal tail and a "fore-paddle" rather than limb.

It appears that the latter types of evidence would certainly support an aquatic mode of life for the metriorhynchids, but it has been illustrated here that the characters possessed by the steneosaurs would not preclude them from sharing a similar mode of life and range of environments. In this context, the concept of one form - one function or one set of forms equals a particular adaptation is modified to produce the concept of: different forms = equal adaptation.

It would seem that neither genera exhibit a morphology which would preclude them from swimming in the marine environment which produced the Oxford Clay. The metriorhynchids, however, possessed certain skeletal features which enabled them to swim at speed.

A greater degree of niche overlap would seem to be reasonable, in view of the fact that both genera are found in juxtaposition in the matrix.

Documented information about the levels of parental care sustained by recent crocodilians (Attenborough 1979) would seem to necessitate these animals remaining relatively close to the nesting site during periods of

incubation, hatching and early juvenile stages. If this is applicable to the Callovian Crocodiles it will restrict the range of niches in the marine environment which they can occupy, whilst maintaining some kind of vigilence over their eggs and young.

The feasibility of viviparity in the metriorhynchids does not seem compatible with the retention of a hind leg, without any indication of modification of this limb to a paddle.

This fact may help to explain the distribution of the crocodiles in relation to the environmental reconstructions outlined in the following chapter.

CONCLUDING STATEMENTS

It has become apparent, through this study, that inaccurate, and in some cases, exaggerated ideas about the ecology and mechanics of these animals has resulted from cursory examination of material. This situation has been further confused by the application of early ideas uncritically by later workers.

This chapter has attempted to show the range of information that can be deduced, the methods employed, and the limitations which are necessarily imposed when working with vertebrate fossil material.

Using this new information, some original thoughts, and insight into the mechanics and functions of the Callovian Crocodiles have been generated. These can be correlated, in turn, with information about the environments they inhabited (contained in chapter 3). Using this interdisciplinary approach, it is hoped to maximise our knowledge of the ecology of the two genera, Steneosaurus and Metriorhynchus.

ECOLOGY

INTRODUCTION

Aside from minor variations in lithology (and quite marked variation in some zonal thicknesses) the Oxford Clay, as seen in the quarries between Peterborough and Aylesbury, appears similar in the suite of lithologies and faunas it presents. The known record of crocodilians would appear to indicate a concentration around the Peterborough area, where many pits were, and are, clustered. In this region the Callovian crocodiles are, together with Ophthalmosaurus, amongst the most numerous elements of the vertebrate fauna (E. T. Leeds 1956). Extremely rare occurrences of crocodiles have been recorded as one traces the outcrop southwards where, in direct contrast, ichthyosaurs and plesiosaurs begin to dominate the vertebrate faunal associations (Delair pers. comm. 1978). The apparent geographic zonation of the crocodiles must be considered in the light of the information presented in chapter 1.

Palynological assemblages have not been described from the Lower Oxford Clay of the East Midlands with the exception of Woollam (1977 MSc. thesis unpubl. Sheffield University). Early work on the Oxford Clay was carried out by Sarjeant (1961, 1962a) on assemblages from Yorkshire and Dorset. No subsequent studies have been published.

The purpose of Woollams' work was to attempt a gross palynological study of the Middle and Upper Callovian and Lower Oxfordian deposits in the East Midlands and to determine whether any marked changes in the palynological assemblages from these sediments occurred in the Lower Oxfordian. In Central England these deposits are represented by most of the Lower, all of the Middle, and part of the Upper Oxford Clay.

In the context of this work, palynological analysis of "crocodile bearing" Lower Oxford Clay sediments has been carried out in an attempt to use palynology to assist in the resolution of the ecology of the marine crocodiles.

METHODS

SAMPLING TECHNIQUE

The sampling technique for palynological analysis is based on the patterns of distribution of crocodilian remains as recorded at present. Difficulties inherent when working with museum collections include the inaccurate stratigraphic and geographic location of specimens, and the comparative rarity of fossil vertebrates. The latter factor becomes very significant when attempting to establish and understand the original distribution of the crocodiles, as this will determine the areas of most detailed sampling of the Oxford Clay.

The crocodiles are concentrated in the sediments belonging to the jason Zone and overlying lowest Subzone of the coronatum Zone, the obductum Subzone, thus defining the thickness over which sampling would be conducted.

As indicated overleaf, although arguably the most uniform of deposits in the whole of the British Jurassic, the Oxford Clay does exhibit considerable lateral variation in thickness in the jason Zone and, to a much lesser extent, in the obductum Subzone.

Sampling intervals have been based on:

a. The thickness of relevant Zones at a particular locality. The thickness of the jason Zone increases southwards and, therefore, for practical reasons the sampling interval was coincidently increased.

b. The thickness and variety of lithological units. Different lithologies are normally indicative of changing environmental conditions and, therefore, rapidly changing lithological suites were sampled over narrower intervals to maximise information about the environments of deposition.

The consideration of b. superimposed on a. lends flexibility to the sampling system.

The succession is most condensed in the Peterborough area and, in addition, this is the locality from which the vast majority of crocodile specimens have been collected, and thus it was, therefore, sampled throughout at intervals of 25 cms.

Samples were also taken from exposures at Stewartby, Bletchley and Calvert London Brick Company Pits (see fig. 47). For sampling intervals, thicknesses of the succession and suites of lithologies at these localities, see figs. 49 - 52.

All the samples are correlated with the detailed biostratigraphy erected by Duff in 1975 (as outlined in fig. 53) and can, therefore, be chronologically related to each other with great accuracy. Application of the techniques outlined in this chapter will make it possible to establish whether there is a contemporary environmental change at the various geographic localities which might explain the distribution pattern of the crocodiles.

PREPARATION TECHNIQUES FOR PALYNOLOGICAL ANALYSIS

The objective during preparation is to extract and isolate the organic microfossils (palynomorphs) from the sample and to obtain a residue which is free from mineral and amorphous organic material, thus enabling easy examination and identification of the palynomorphs (Woollam 1977).

The technique outlined below is based on that of Woollam (1977), modified at various stages, as a result of experimentation in this field.

The only material which seems impossible to remove at present is kerogen, which was present in most of the samples in varying, and usually quite high, proportions, often partially or wholly obscuring the palynomorphs. The presence of kerogen also "dilutes" the concentration of palynomorphs for a given slide or area of a slide, so that the quantitative analysis

is necessarily based on many more slides (which lengthens the analysis time). I support the conclusions of Woollam (1977) that limited ultrasonic treatment, although causing some fragmentation of palynomorphs, is the best method for breakdown of kerogen to a reasonable working size, without the selective removal of certain palynomorphs (which would certainly be the result of oxidation of the residue).

The sample was initially broken into small fragments to enable effective reaction with acids. All of the samples were soft enough to be broken by hand. The small pieces of clay were placed in a glass or polythene beaker and then dilute, followed by concentrated Hydrochloric acid was added to remove any carbonate present. The addition of a measure of concentrated acid confirmed that the removal of carbonate was complete.

After the reaction had ceased, the residue was neutralised by decanting off the liquid and washing several times with distilled water. The neutralised residue was then placed in a polythene container (which had been sterilised with chromic acid) and concentrated Hydrofluoric acid added, causing complete breakdown of mineral matter. This was left for approximately ten days (during which time the Hydrofluoric acid may be changed several times to increase the speed of breakdown of silicate chains in the clay minerals). The residue was then neutralised by decanting off the liquid and washing repeatedly with distilled water.

The residue was then boiled in concentrated Hydrochloric acid which aided in the removal of background amorphous organic material. The acid was then decanted off, and the residue centrifuged several times with water to concentrate and neutralise the residue.

Following concentration, the residue was passed through a 125 mu sieve to remove any coarse material; this was discarded, as none of the

samples in this fraction contained any palynomorphs. The remaining material was divided into three size fractions: greater than 40mu, between 40 and 20mu, and less than 20mu by sieving. Separation of greater and less than 40mu fractions, facilitates more rapid sieving, reducing the frequency of clogging of the nylon mesh sieves by the clay particles. The two fractions were subsequently mixed together.

The fine fraction (i.e. less than 20mu) was washed through a sintered glass funnel number 4, so removing material of less than 8mu, which was discarded, and the remaining fraction was placed in a glass storage tube.

The material was now ready for mounting on glass slides for microscopic examination. Two sets of slides were initially produced, for the two size fractions (less than and greater than 20mu) although in practice it was discovered that only the larger fraction contained a workable sample of identifiable palynomorphs, because of the general size of Mesozoic genera.

Standard mounting techniques using Cellosize (hydroxethyl cellulose) and Canada Balsam were employed for making the mounts, which will not dry out and are, therefore, permanent.

Examination of the slides

Quantitative analysis

The process leading up to the preparation of slides containing concentrations of pollen is essentially one of sequential sampling and sub-sampling. Each sampling stage involves a successive approximation and hence decrease in accuracy of the ultimate representation (Moore & Webb 1978). The final pollen count must be determined that will most efficiently estimate the palynological proportions on the sample slides. The size of the count taken in the work was determined by reference to the recommendations outlined in Moore & Webb (1978 chapter 6 pp. 78 - 96, figs. 6 and 7, p. 88).

Numbers of spores, pollen and plankton were thus counted during a traverse of sections of a number of slides, until 250 individuals had been counted (this being the level of "cut-off" shown by Moore & Webb to give an adequately realistic representation of the diversity and proportions of genera present.

The spore/pollen/plankton ratio, and the relative percentages of particular genera of the above, were then determined as shown in tables

LITHOLOGIES COMPRISING THE LOWER OXFORD CLAY AT LOCALITIES SAMPLED

The biofacies (sensu Duff 1975) which are combined together in various suites at the four localities sampled are described below. These descriptions are a digest of part of Duff's (1975) analysis of Lower Oxford Clay facies in the East Midlands.

Silts and silty clays

These occupy a transitional zone between the Kellaways Rock and the Oxford Clay (the "transition beds") and are characterised by infaunal and epifaunal suspension feeders, while deposit feeders are of minor importance. This indicates an appreciable degree of current action and resultant quantities of suspended food in the environment. The degree of current activity is evidenced by the sedimentary structures (see below) and would produce well aerated water. The combination of well aerated water and a rich food supply promoted the establishment of the diverse fauna in these sediments, dominated by suspension feeders. The presence of some micro-cross laminations in the sediment is indicative of shallow water current action as is the high degree of bioturbation and burrowing of the sediment.

Bituminous shales

These are well laminated shaley clays which comprise the bulk of

the Lower Oxford Clay. Deposit feeders dominate the faunal content of large thicknesses of this facies, known by Duff as the "Deposit feeder bituminous shales". These deposit feeders consist mainly of pendant bivalves (sensu Duff, these bivalves attached themselves to suspended organic material i.e. water plants in the water e.g. Bositra and Melleagrinella) the "true" benthos being dominated by deposit feeders including Procerithum, Mesosacella, Nuculoma and the tolerant suspension feeder Lingula.

Duff argued that this facies was the least well aerated of the facies encountered in the Lower Oxford Clay because of the "impoverished benthos" composed of the most tolerant deposit and suspension feeders, and gives as evidence for the quiet nature of the sedimentation the presence of articulated crustacea and ophiuroids. The great majority of articulated vertebrate skeletons which comprise the Leeds Collection were collected within this facies.

Duff recognised two other biofacies within this lithology, distinguishable on the basis of their fauna, Grammatodon bituminous shales and foraminifera rich bituminous shales, neither of which are important in the context of this work.

Of the four shell beds recognised by Duff, two are encountered in lithologies sampled in this work, and are classified by him according to their composition, as follows:

Nuculacean shell beds

These have a faunal composition similar to the deposit feeder bituminous shales. Duff suggested that their stratigraphic location and composition represented pauses in the deposition of normal deposit feeder facies. They often contained abundant wood fragments and disarticulated bones.

Gryphaea shell beds

These are restricted to the transition beds. Gryphaea accounts for 62% of the fauna; 28.7% of the remainder includes 12 species of suspension feeder and the remaining 8.5% is composed of three species of deposit feeders. This faunal association, therefore, is characterised by suspension feeders indicating the character of the environment that they were inhabiting (see p. 142). The fauna is similar to that of the beds in which the shell bed occurs i.e. this bed is a shell concentrate. Duff suggests that this shell bed may be, at least in part, a transported assemblage, citing as evidence the presence of disarticulated bones and bivalve shells. In addition, the presence of oysters suggests that this facies was deposited in shallower water than the bulk of the Lower Oxford Clay, with periodic wave scouring.

Blocky claystone

This lithology is known only from the jason Subzone at Calvert (Bed 3B, Duff 1975). It is "a distinctive light grey, rather plastic, non-fissile clay, with many black organic fragments spread throughout it" (Duff 1975 p. 471). It occurs within deposit feeder bituminous shales and is similarly dominated by pendant bivalves (58% of the fauna). The remainder of the fauna comprises infaunal deposit and suspension feeders; Lingula and Solemya are characteristic members of the latter group. There is a limited diversity of faunal types in this facies. Thus in this biofacies we see an unusual lithology coupled with an unusual fauna.

Relationship between the biofacies

Superimposed on local variations in the grossly similar succession at the four pits sampled, is a marked southward increase in thickness (particularly in the jason Zone) as shown in fig. , and a coincident decrease in the number and thickness of shell beds.

Since most of the thickness variation is seen in the jason Zone, Duff argues that, during the deposition of the initial Subzones of the Lower Oxford Clay, conditions were more variable and controlled by local configurations of the sea floor (i.e. topography), but that by obductum Subzone times, conditions had stabilised over the area producing a more uniform thickness of sediment. The transition beds are best developed at Peterborough and well developed at Bletchley.

During the initial phases of sedimentation, Duff envisaged variable current activity. At this time, periods of increased current activity produced Gryphaea shell beds and micro-cross laminated silts, and were intercalated with quieter phases in which the bituminous shales were deposited. The alternating environments of deposition were attributed by Duff to fluctuations in sea level. Phases of shallowing resulted in increased current activity, while the influence of the offshore clay facies, with increased distance from shore and possibly water depth, produced the bituminous shales. The gradual recession of the shore line during deposition of the transition beds eventually allowed the establishment of quieter conditions in which the bituminous shales were laid down. For the duration of the bituminous shale deposition, the prevalence of quiet bottom conditions and poor water circulation produced an impoverished benthos dominated by pendant bivalves.

The obductum Subzone at Stewartby contains well developed shell beds and only a relatively thin deposit of bituminous shales. Throughout the entire region, the end of the obductum Subzone is coincident with the development of shell beds.

Duff attributes the many small scale alternations of lithology within the Lower Oxford Clay to relatively shallow water deposition where slight changes in water depth could have a marked effect on the hydrographic conditions.

LOWER OXFORD CLAY SPORES, POLLEN AND DINOFLAGELLATES

By surveying the literature on Jurassic Palynology (for a discussion of this see Filatoff 1975), and reference to the work of Woollam (1977) and Windle (pers. comm. 1978-80), a list of the genera of spores, pollen and dinoflagellates one might expect to occur in the Lower Oxford Clay was compiled as follows:

SPORES

Calamospora

Retusotriletes

Stereisporites

Krauselisporites

Todisporites

Biretisporites

Deltoidospora

Mantonisporites

Triplanosporites

Cibotiumspora

Obtusisporis

Concavisporites

Osmundacidites

Baculatisporites

Verrucosisporites

Anapiculatisporites

Concavissimisporites

Varirugosisporites

Rubinella

Leptolepidites

Uvaesporites

Neoraistrickia

Ceratosporites

Lycopodiacidites

Lycopodiumsporites

Staplinisporites

Foveosporites

Sestrosporites

Ischyosporites

Gleicheniidites

Densoisporites

Neveisporites

Polycingulatisporites

Duplexisporites

Contignisporites

Leavigatosporites

Punctatosporites

POLLEN

Inaperturopollenites

Callialasporites

Cerebropollenites

Perinopollenites

Cycadopites

Alisporites

Vitreisporites

Pityosporites

Podocarpidites

Parvisaccites

Exesipollenites

Classopollis

ACRITARCHS

Micrhystridium

Veryhachium

Leiosphaeridia

DINOFLAGELLATES

Sentusidinium

Caligodinium

Pareodinia

Valensiella

Ellipsodictyum

Ctenodinium

Microdinium

Lithodinia

Gonyaulacysta

Endoscrinium

Adnatosphaeridium

A record of the genera recorded in the present study is shown in Results (1). Only those genera actually recorded in this work have been dealt with in the systematics section in appendix 4.

SYSTEMATICS

A survey of a selection of palynological literature (Couper 1958, Dettman 1963, Guy 1971 and Filatoff 1975) indicates that there are two types of classification systems accepted for fossil spores and pollen.

The first system designed by Potonié & Kremp in 1954, outlined in Dettman (1963) and modified by Dettman (1963) and Guy (1971), is a morphological system. A variety of morphological classifications have

been presented to date (for a discussion of these see Dettman (1963) in which spores and pollen grains which share similar morphological characters are placed together in groups. This classification system makes no attempt to determine the possible phyletic significance of these characters. The system (outlined in part in figs. 55,56) after Dettman (1963) consists of a series of ranked categories, rather similar to a key system, where each particular rank must be composed of mutually exclusive taxonomic units, which will be based on one diagnostic character only. This principle is of fundamental importance to the design of an unambiguous system. This type of system was designed primarily as a tool to facilitate data retrieval (by stratigraphers) and cannot, by design, provide information of an evolutionary or ecological type.

In the second system, genera are arranged in groups that have some distinctive morphological characters that are considered to indicate phyletic affinity. Deductions about the botanical affinities are based on fossilised parent floras and their associated spores, and morphological comparisons between spores and pollen in situ in living plants and dispersed fossil spores and pollen grains.

In this context Couper (1958) compiled a catalogue of spores and pollen grains isolated from fructifications of 88 species of Mesozoic plants, as a prerequisite to his study of dispersed spores and pollen grains from Mesozoic sediments. These "associated" spores and pollen grains were compared with those of living plants to determine their botanical affinities.

Harris (1961) similarly worked extensively on Jurassic floras from Yorkshire.

Dettman's revised classification system (1963) was based on the following diagnostic characters in descending order of rank (for spores):

1. aperture character
2. wall stratification
3. equatorial thickenings and/or extensions of the spore wall
4. sculptural features

and for pollen grains:

1. presence, absence and character of the aperture
2. presence and number of sacci

These classification systems are summarised in figs. 55 and 56. These figures indicate that the presence or absence of, and details of, sculptural features of the exine of the spores are used to classify Infraturma within the Subturma Azonotriletes, and that the presence and number of sacci are used similarly to classify pollen grains at Subturma level. These morphological characters will also, at least partially, determine the pattern of dispersal of the grains in the depositional environment that produced the Lower Oxford Clay. An explanation, therefore, of Infraturma classes have been included where they are determined on the basis of the above features (in appendix 4).

The genera identified in this work, are classified according to the morphological classification system in appendix 4, and the botanical affinities are indicated where known (Couper 1958, Harris 1961, Filatoff 1975). The full reference to each genus is also included, as is a reference to a published illustration. Line drawings for all the genera listed on pp. 146 - 148 are included in fig. 65.

The major source of reference used was the Genera File of Fossil Spores (Jansonius & Hills 1976) where the full diagnosis for each spore and pollen grain is located. This was supplemented by other works, notably: Couper (1958): Harris (1961): Potonié (1962): Dettman (1963): Guy (1971): Pocock (1970): Filatoff (1975).

The descriptive terminology used in the above classification and in the Results (1) is included in appendix 4 in glossary form (after Dettman 1963).

The main sources of reference for the dinoflagellates here studied were the following works:

Sarjeant (1961, 1962 a, 1966, 1970 c, 1974): Downie & Sarjeant (1964): Downie (1957): Downie, Evitt & Sarjeant (1963): Norris & Sarjeant (1965): Evitt (1969): Riley & Sarjeant (1972): Williams & Sarjeant (1967).

A classification of the genera identified in this study at family level (after Sarjeant 1974) is included in appendix 4.

PREVIOUS ATTEMPTS TO USE PALYNOLOGY IN THE RECONSTRUCTION OF PALAEOENVIRONMENTS

Chaloner and Muir (1968) showed that changing conditions of deposition could affect the enclosed spore (sensu Chaloner & Muir loc. cit.) population in various indirect ways. This was a further development of earlier work by Muir (1964), who argued that the composition of the palynological assemblage was not independent of the sedimentary facies (as was commonly believed at that time). Muir investigated a series of factors which apparently controlled the relative proportion in which the different components of the regional flora would be represented in the sedimentary facies indicative of a particular depositional environment. The spores and pollen analysed in the present work must have been, as were many of those studied by Muir, incorporated into a sediment produced in an environment which totally contrasts with that in which the parent plants were actually living. They have, inevitably, undergone some form of transport to appear in those sediments. Spores and pollen incorporated in "non-

marine" sediments e.g. deltaic deposits and coals, may be deposited virtually in situ.

The dispersal mechanisms involved in the transportation of the spores to the site of fossilisation would be wind and, in the case of this study, subsequently water currents.

Müller's work (1959) is a good place to begin an analysis of the mechanisms which might be controlling the composition of the Oxford Clay assemblages. Müller worked on the palynology of recent sediments from the Orinoco Delta and shelf, and found that the positions of the delta coast line and the mouths of estuaries were indicated by an increase in the total pollen content as one moved towards the main pollen source and by a coincident decrease in dinoflagellate abundance. Within this general trend, however, existed a number of apparent anomalies e.g. the percentage of mangrove pollen was shown to increase as one moved progressively off shore - away from the swamp. Chaloner & Muir argued that this contradictory situation was a reflection of the fact that the mangrove pollen grains were so minute that they floated in the air and subsequently on the water for longer periods than the other pollen types and were thus transported further out to sea. Müller found that crossing the delta shore line, although not expressed by a distinct lithological change, was registered by an abrupt increase in the total pollen content. This was accompanied by a change in the character of the palynological assemblages as one moved across the delta, with the percentages of certain pollen genera reflecting the local dominance of particular floral swamp associations.

Müller's analysis of the variation in pollen content of the surface and core sediments provided a model of the factors affecting the transportation and sedimentation of pollen in the deltaic and near-shore environments, affording a means of estimating the relative

importance of wind and water transport. He argued that his data could be extrapolated to ancient sediments:

"the distribution of pollen and other microfossil groups can be utilised in studies of depositional environments and are valuable in facies recognition, and in the palaeogeographical reconstruction of ancient sedimentary basins ..... The recognition of palynological provinces makes it possible to distinguish rather sharply the characters of several major types of environment. The consistent decrease in total pollen content ..... indicates the possibility of reconstructing positions of shore lines. In this respect palynology can make a valuable contribution to palaeogeographic interpretations" (1959 p. 29).

Müller's environmental analysis is a static one, in the sense that he was able to distinguish the spatial relationships between palynological provinces and the depositional environment (i.e. the facies that their pollen became incorporated in) by analysing the surface sediments.

Comparable situations to the above, but involving only wind transport, were demonstrated by Hedberg (1956) and Tauber (1965). The latter author constructed a model to account for the various mechanisms whereby pollen could be deposited in a lake flanked by vegetation, arguing that the representation of a particular form in the lake sediments would depend on:

a. the stature of the parent plant and, consequently, the region of air currents into which the pollen would be released.

b. the morphological features of the grains which would assist in their wind dispersal: the "dispersal efficiency".

Neves (1958) and Muir (1964) have made important studies of Palaeozoic and Mesozoic spore assemblages respectively, sampled through a lithologically varied vertical sequence of sediments.

Neves calculated the relative abundance of spore and pollen genera from Namurian cyclic sediments, comprising a coal seam and associated non-marine shales and marine shales in a vertical sequence. The largely similar assemblages which characterised the coal and non-marine shale i.e. dominated by lycopod and filicalean spores, sharply contrasted that from the marine shales which was dominated by the pollen grain Florinites. The parent plant producing the most common spores in the coal and non-marine shale assemblages had been identified as Lepidodendron, while the pollen dominating the marine sediments could be linked to large "conifer-like" trees - the Cordaites (Chaloner & Muir 1968).

Neves argued that the relative abundance of the Cordaites pollen reflected the distribution of these plants at the time of the marine incursion i.e. marginal to the site of marine deposition. Spores which had formed appreciable components of the "coal swamp assemblages" were now strictly limited by the marine incursion.

Chaloner & Muir (1968) offered an alternative mechanism for the above situation, in which the Cordaites dominated assemblage in the marine shale represented an upland Cordaites community, rather than one in immediate proximity to the marine environment. In this instance the spores accumulating in the coal were derived from the coal swamp vegetation i.e. they were deposited in situ. At this time pollen transported by the wind from the upland Cordaites community would form only a negligible proportion of the total spore and pollen assemblage. Large scale inundation of the coal swamp vegetation would result from periodic and extensive marine incursions, to produce the marine shale. All the palynological components of this sediment must have been transported into the depositional environment and, with the severe restriction of the swamp vegetation, now at its maximum distance from

the depositional environment (Chaloner & Muir 1968), the spore rain from the upland Cordaites community, unaffected by the incursion, would form a larger proportion of the assemblage.

Chaloner & Muir accordingly proposed a model in which the spore assemblages "change successively in response to varying proximity and extent of the parent communities brought about by changing base level" (1968 p. 139) (sea level) which is termed by them the "Neves Effect".

Muir's study of spore assemblages in a variety of Middle Jurassic deltaic lithologies (1964) provide results consistent with the interpretation outlined in the Neves Effect. The lithologies ranged from coal seams to marine sandstones, and Muir made spore counts from these rocks and expressed the relationship between spore "lumped groups" and particular lithologies as a series of histograms (later reproduced in Chaloner & Muir 1968 fig. 5.) The "lumped groups" were erected on the basis of knowledge of the botanical affinities of the dispersed spores and pollen as follows:

1. Fern spores e.g. Deltoidospora, Todisporites
2. Bisaccate pollen of pteridosperms and Caytoniales e.g. Alisporites, Vitreisporites
3. Probable conifer pollen e.g. Classopollis, Exesipollenites Tsugaepollenites
4. Monosulcate pollen from Cycadales e.g. Cycadopites

In general, the spore assemblages in terms of these four groups from the same type of lithology were closely comparable, regardless of their stratigraphic position. They apparently showed strong correlation with the environments of deposition evidenced in the lithologies. In the coals, non-marine shales and siltstones, the assemblages were dominated by spores from group 1, with groups 2 and 4 forming a negligible part of the assemblage, and group 3 a small but increasingly

important element as one moved from coal to siltstone facies. In complete contrast, the assemblages obtained from the marine sediments (e.g. the Lower and Upper Lias, Dogger, Scarborough Limestone and Yorkshire Oxford Clay) contained up to a maximum of 83.6% of group 3, the conifer pollen, and it follows that the other groups comprised a very minor part of the assemblage. The deltaic sandstones were somewhat transitional between the silts and marine sediments. The assemblages characterising the coals, shales and silts respectively, seem most likely to represent vegetation colonising and depositing their spores autochthonously in the deltaic sediments. The deltaic sandstones seem to represent material transported into the depositional environment, bringing with it water transported spores; they thus compare more closely with the assemblages from the marine lithologies (Chaloner & Muir 1968).

The marine assemblages comprised spores of plants from the hinterland rather than those of the deltaic swamp (Muir 1964) which must, therefore, have been transported into the depositional environment by wind and water.

This explanation of the distribution of the dispersed spores is supported by the mode of fossilisation of the parent floras. The majority of trilete and monolete spores occuring in high percentages in the coals and siltstones have been found in situ, in ferns which occur commonly as macrofossils in the autochthonous Yorkshire Deltaic sediments (Chaloner & Muir 1968). The dispersed spore genera comprising Muir's group 3 (1964) have never been found in situ, (i.e. in the fructifications of the parent plants) despite the intensive studies of the Middle Jurassic floras by Couper (1958) and Harris (1961). These genera compare closely in their morphology with spores of living conifers (particularly of the family Pinaceae), although this group is

unknown as macrofossils before the Cretaceous (Chaloner & Muir 1968). What is certain, however, is that the spores and pollen which occur abundantly in the marine lighologies described overleaf must have been derived from plants which never occurred as common elements of the delta vegetation, because otherwise we would find the remains of the parent flora alongside the dispersed spores and pollen grains.

Chaloner & Muir concluded that in the Yorkshire Deltaic Series, as in the Coal Measures, "the marine rocks are rich in spores of plants that were apparently growing in a habitat remote from the marine environment" (1968 p. 139).

Muir's work (1964) had showed that Middle Jurassic spore and pollen assemblages were apparently controlled by the lithologies in which they were found, which were, in turn, accepted as being indicative of a particular depositional environment. She had further refined her analysis in 1964 (although this data does not appear in the 1968 publication) by examining the behaviour of individual genera of spores in different lithologies and found that, on the basis of their occurence, she could determine six groups, of which the following are of relevance to the present study:

1. Pityosporites and Tsugaepollenites, which occur only in marine sediments. Because these pollen grains had never been recorded in situ, Muir concluded them to be derived from the hinterland.

2. The spores and pollen in this group occurred in maximum numbers in marine sediments and only sporadically in the coals. Genera relevant to the present study have been selected from Muir's data as follows:

Lycopodiumsporites Lycopodialean spore

Classopollis which is most abundant in coarse grained marine rocks and diminishes sharply as the grain size decreases.

Cycadopites

Exesipollenites

Alisporites

These two groups were, therefore, abundant in marine rocks and were, in Muir's opinion, produced by a hinterland flora i.e. a coniferalean type flora.

3. The following genera occurred approximately equally in marine and deltaic deposits:

Cycadopites; Triplanosporites; Varrirugosisporites; Alisporites; Cerebropollenites; Ischyosporites; Deltoidospora; Concavisporites

and were produced by a parent flora colonising the delta floodplain.

Thus, in these works, we see strong evidence for the correlation between the character of the spore assemblage and particular lithologies, and some of the mechanisms suggested to account for these relationships. In these works a series of the situations as analysed by Müller (1959) are superimposed on one another, where successive samples show palynological assemblages indicative of changes at that geographic locality, with time, in the depositional environment. Thus an area which was near shore will, after a marine transgression, become further offshore because the transgression will change the position of the coastline. Thus, although always sampling at the same geographic locality, the marine transgression and sedimentation in a new depositional environment is represented by the change in lithology in the next higher stratigraphic horizon.

If palynological analyses are carried out on a series of lithologies contained in a vertical sequence at one geographic locality a dynamic picture of environmental change with time at that locality can be obtained because, as we have seen, Neves (1958), Muir (1964), Chaloner & Muir (1968), the changing environments exert an influence over the parent floras.

If sediments from chronologically equivalent stratigraphic horizons at different geographic localities are sampled, one can, by using the same techniques, obtain an impression of synchronous depositional environments and their spatial relationships to one another.

In this context, a detailed analysis was carried out by Windle (1980) who made spore and pollen grain and microplankton counts through vertical sequences of cyclic sediments at various localities in the Hampton Marley and Sharps Hill Formations and the Fimbrata-Waltoni Clays (Bathonian) in the Oxfordshire region. He computed the average relative percentages of spore,pollen and plankton genera from all these stratigraphic horizons, selected values of which are shown in table 23 (where values from all the geographic localities are combined to give a single set of figures). These values are grouped on the basis of the environments of deposition they were indicative of, which were evidenced by the lithologies from which they were obtained. In this instance group 4 represents the assemblage derived from rootlet bearing clays, group 3 from brackish water clays, group 2 was obtained from fully marine clays immediately beneath the brackish water clays, while group 1 represents the assemblages derived from fully marine sediments some considerable distance beneath the brackish water clays i.e. separated from the brackish water clays by a greater stratigraphic interval.

Woollam (1977) applied these principles to Callovian and Lower Oxfordian Sediments from the East Midlands of England, although these sediments did not exhibit obvious lithological changes. Basing his conclusions on the premise that the relative proportions of miospores (i.e. spores and pollen) were a direct result of the distance of a locality from a major land mass, he argued that the relatively high proportions of miospores to microplankton throughout the Callovian and

Lower Oxfordian in this region indicated the strong influence of the London Platform in the Oxfordshire shallows at this time. Details of Woollams' sampling intervals and methods are discussed in pp. 180 - 181, but it is relevant at this point to emphasise that his "spore" counts were taken from closely similar lithologies and that he computed the total spore/pollen, and plankton numbers only, so that he drew no quantitative distinctions between component genera of this total number.

A MODEL FOR THE LOWER OXFORD CLAY

The associations between spores, pollen, microplankton and lithologies as documented by Neves (1958), Müller (1959), Muir (1964), Chaloner (1968), Tauber (1965), Chaloner & Muir (1968), Woollam (1977) and Windle (1980) have been synthesised to produce a model which is applicable to the Lower Oxford Clay sediments analysed in the present study.

In the first instance the relative percentages of spores and pollen to dinoflagellates were counted and the variation in this relationship through a vertical sequence of subtly changing lithologies was considered. The analysis was then further refined and the individual genera comprising the spore/pollen and dinoflagellate assemblages were counted. The spore and pollen genera were subsequently grouped on the basis of their botanical affinities (in a similar way to Muir 1964) and size and morphology (as shown in pp. 166 - 168) where in general it was seen that the spore and pollen produced by the same kinds of parent plants shared similar morphologies.

In marine sediments the percentage representation of a particular spore or pollen genus has been shown to be the result of the distribution of the parent flora with respect to the depositional site "which is apparently at least partially due to the movement of the shoreline"

(Chaloner & Muir 1968 p. 145) which is in turn reflected in the changing lithologies.

The spores and pollen occurring in the Oxford Clay must inevitably have undergone transport, since they are now incorporated in sediments produced in an environment which could not possibly be colonised by vegetation. Müller (1959) showed that the two dispersal agents were wind and, subsequently, water currents. The size and morphology of the palynomorph will determine the extent of this transportation (as illustrated by the distribution of mangrove pollen by Muller) who determined that water borne palynomorphs in the size range between 2 - 64 microns settle at the same rate as silt particles which have a comparable diameter. The relative abundance ot microplankton was shown by Müller and Williams & Sarjeant (1967) to increase with distance from shore.

Sarjeant (1962 a) proposed that the morphology of the dinoflagellate genera could be of use in determining the type of marine environment in which they occurred. Forms with simple ornamentation i.e. low crests and short spines, seemed to correlate with high energy, "near shore" marine environments which apparently necessitated robust, resiliant forms.

According to the "Neves Effect" (Chaloner & Muir 1968 p. 139) in the different lithologies comprising the Lower Oxford Clay here analysed, variation in the composition of the palynological assemblages incorporated into the sediments will be at least partly due to migrations of the shoreline position, and coincident change in the depositional environment. The results of the palynological analysis can subsequently be combined with data on the invertebrate (Duff 1975) and vertebrate faunal assemblages (the present work) and with details of the bio-stratigraphy and sedimentology of the Lower Oxford Clay to reconstruct

the ecology of the Callovian Crocodiles within the context of the Lower Oxford Clay palaeogeography.

RESULTS

RESULTS (1)

The genera listed on pp. 146 - 148 were organised into initial groups on the basis of their botanical affinities which are, to a large degree, reflected in their similar morphologies.

An indication is given below of those genera recorded from the Lower Oxford Clay in the course of this study and those which were not found, and a qualitative indication of their relative abundance given as follows:

R rare

UC uncommon

OC occasionally common

C common

VC very common

GROUP NO.	SPORES FOUND	SPORES NOT FOUND
1		Calamospora
		Retusotriletes
		Stereisporites
		Krauselisporites
2	Todisporites R	
3	Deltoidospora C	
	Mantonisporites R	
	Biretisporites R	

GROUP NO.	SPORES FOUND		SPORES NOT FOUND
4	Triplanosporites	OC	
5	Obtusisporis	UC	
	Cibotiumspora	R	
6	Concavisporis	OC	
7	Osmundacidites	UC	Baculatisporites
			Verrucosisporites
8			Anapiculatisporites
9	Concavissimisporites	C	
10	Varirugosisporites	R	
11			Rubinella
12			Leptolepidites
13	Uvaesporites	UC	
14			Neoraistrickia
			Ceratosporites
15	Lycopdiacidites	UC	
16	Lycopodiumsporites	OC	
17	Staplinisporites	UC	
18	Foveosporites	R	Sestrosporites
19	Ischyosporites	C	
20			Gleicheniidites

GROUP NO.	SPORES FOUND		SPORES NOT FOUND
21	Densoisporites	R	
22	Neveisporites	R	Polycingulatisporites
23			Duplexisporites
			Contignisporites
24	Leavigatosporites	R	Punctatosporites

GROUP NO.	POLLEN FOUND		POLLEN NOT FOUND
25	Inaperturopollenites	VC	
26	Callialasporites	VC	
27	Cerebropollenites	OC - C	
28	Alisporites	C - VC	
29	Vitreisporites	UC	
30	Pityosporites	C	
	Podocarpidites	C	
31			Parvisaccites
32	Perinopollenites	C	
33	Cycadopites	UC	
34	Exesipollenites	C	
35	Classopollis	VC	
36	Broken bisaccates	C	

GROUP NO.	ACRITARCHS FOUND	ACRITARCHS NOT FOUND
37	Leiosphaeridia C	
38	Micrhystridium R	Veryhachium

GROUP NO.	DINOFLAGELLATES FOUND	DINOFLAGELLATES NOT FOUND
39	Sentusidinium VC	
40	Caligodinium C - VC	
41	Pareodinia C	
42		Valensiella
43		Ellipsodictyum
44	Ctenodinium C	
45		Microdinium
46	Lithodinia C	
47	Gonyaulacysta VC	
48		Endoscrinium
49	Adnatosphaeridium R	
50	Broken dinoflagellates OC	

These data were then further grouped according to their botanical affinities, morphology and occurrence in the sediments analysed (i.e. if they were abundant and well distributed enough to work with) rather similarly to Muir (1964), reproduced in Chaloner & Muir (1968 p. 138 fig. 5). A glossary of the descriptive terms used in this section are included in appendix 4.

GROUP 1	SIZE
LYCOPOD SPORES	
Staplinisporites	39 - 45u
Densoisporites	46 - 74u
Lycopodiumsporites	37 - 54u
Uvaesporites	41 - 53u
Varirugosisporites	67 - 76u
Neveisporites	46 - 58u

Reniform, reticulate or verrucate spores, with variously developed ornament but not prominent, and with exine of moderate thickness.

GROUP 2	
FERN SPORES (Groups 2 - 4 inclusive)	
Dicksoniaceae/Cyatheaceae	
Deltoidospora	34 - 72u
Obtusisporis	46 - 57u
Concavisporites	28 - 57u
Cibotiumspora	43 - 59u
Triplanosporites	30 - 50u

Smooth to scabrate spores, the exine may be folded.

GROUP 2A	
Schizaceae/Dicksoniaceae	
Concavissimisporites	52 - 81u

Heavily ornamented spores, with a thick verrucate exine.

GROUP 3	
Osmundaceae	
Osmundacidites	37 - 67u
Todisporites	52 - 61u

Smooth to scabrate or granulate spores with a thin exine.

GROUP 4 SIZE

Schizaceae

Ischyosporites 34 - 93u

Heavily ornamented spores with a very thick exine.

GROUP 5

CONIFER POLLEN (Groups 5 - 11 inclusive)

Cupressae/Taxaceae/Taxiodaceae

Inaperturopollenites 62 - 92u

Large one-layered grains, the exine is smooth and characteristically folded.

GROUP 6

Auraucariaceae

Callialasporites 56 - 91u

Monosaccate pollen grains, the exoexine is scabrate to microgranulate.

GROUP 7

Pinaceae/Podocarpidaceae

Pityosporites 50 - 75u

Podocarpidites 50 - 75u

Pteridosperm

Alisporites 74 - 98u

Bisaccate pollen grains.

GROUP 8

Pinaceae

Cerebropollenites 44 - 76u

Polysaccate grains, with multiple small convolute sacci.

GROUP 9 SIZE

Cupressae/Taxaceae/Taxiodaceae

Exesipollenites 23 - 36u

Small grains, with smooth to finely scabrate ornament.

GROUP 10

Chierolepidaceae

Classopollis 31 - 37u

Small grains with an ornament of annular thickenings.

GROUP 11

Cupressae/Taxaceae/Taxiodaceae

Perinopollenites 30 - 55u

Loosely fitting exoexine which is thin and smooth and often folded.

GROUP 12

Acritarchs

Leiosphaeridia

Simple, laevigate spherical bodied acritarchs.

GROUP 13

DINOFLAGELLATES (Groups 13 - 15 inclusive)

Sentusidinium Caligodinium

Ctenodinium

Proximate cysts of variable morphology often spinose and showing crests ornamented with short spinelets corresponding to the tabulation, but without large processes.

GROUP 14

Lithodinia

Gonyaulacysta

Proximate cysts, where the tabulation is reflected in crests which may

be ornamented by short spinelets, but without large processes.

GROUP 15

Pareodinia

Proximate cysts, laevigate, showing no indication of tabulation, and with an apical horn.

RESULTS (2)

The relative percentages of the spore, pollen and plankton genera counted from each locality are outlined in tables 15 - 18. The relative percentages of the 15 groups shown in Results (1) which were derived from the above data are presented in tables 19 - 22 and figs. 49 - 52. The latter relate scaled stratigraphic sections for each pit, including detail of stratigraphy and important invertebrate faunal elements which characterise the succession, with the sample numbers designated for this work. The sample numbers are correlated with the bed numbers designated by Duff (1975) in the erection of his bio-stratigraphy, outlined in fig.53 (after Duff 1975) and presented in full in his unpublished Ph.D thesis (Leicester University 1974).

This means that samples from all four quarries analysed in this work can be correlated with a high level of chronological accuracy to each other, and to their respective lithologies.

Based on the above results, the relationships expressed qualitatively in fig. 57 are proposed. These are similar to the relationships shown to exist in the Bathonian (Windle pers. comm. 1980) as shown in table 23 (composed from data supplied from Windle's results). A more detailed analysis of these values is included in Results (6).

RESULTS (3)

The data presented in tables 15 - 18 and figs. 49 - 52 incorporated a range of values of the relevant percentages for selected spores, pollen and microplankton, and it was possible to segregate them into four comparatively well defined palynological "associations" (1 - 4 as indicated in table 24).

The ranges chosen for each association (as shown in table 24), which were based on the total range of values for a particular genus, the magnitude and detail of its variance between samples taken throughout the succession at each locality, and the values indicated in table 24 were found to be associated as indicated in tables 24a - 24d.

This, then, is the method chosen to present the character and variation of the palynological assemblages in all the samples taken. In each sample number there is, clearly, a mixture of groups but, within this pattern, some trends are evident.

In the topmost samples at all the quarries there is a predominance of values corresponding to groups 1 and 2, whereas the basal samples at Peterborough and Stewartby, in particular, clearly show a progressive change from samples dominated by values corresponding to groups 1 and 2, to those dominated by assemblages indicative of groups 3 and 4. The basal samples at Calvert, taken in the "Blocky Claystone" facies (Duff 1975), show a distinctive combination of groups 1 and 2 with a sharp junction between samples 11 and 12, the lithological junction between the Blocky Claystone and the overlying bituminous shales.

Reference to previous work (outlined in pp. 151 - 160) and discussions on Bathonian data (Windle 1980 pers. comm.) presented here in table 23 (after Windle 1980) would suggest that these four groups have some environmental significance and relevance.

Certain genera and groups of palynomorphs have been shown to become the dominant members of the palynological assemblage at particular distances offshore so that, in this context, group 1 represents the "nearest shore environment" and groups 2, 3 and 4 progressively further "offshore environments".

The summed totals of the group values presented in tables 24a - 24d are shown in tables 25 - 28 . If group 4 is indicative of the furthest "offshore" environment, the highest of these summed values will represent the transgressive maxima and the lowest, the regressive phases, the stratigraphical position of these summed values (and the depositional environments they indicate) being given by the relationship between the sample number and the bed numbers for the succession (Duff 1975).

RESULTS (4)

COMPARISON BETWEEN THE PALYNOLOGICAL RESULTS AND LITHOLOGIES AT THE LOCALITIES SAMPLED

Peterborough

The lowest horizon sampled at this locality, the endodatum Subzone of the calloviense Zone, comprised micro-cross laminated silts and sandy silts with occasional clay intercalations, which graded upward into shaley clay with a silt content.

The lowest part of the jason Zone, the medea Subzone, comprised shaley clay, silty in part, with intercalated shell beds and, towards the very top of this Subzone, we see the introduction of a darker green clay which grades up into well laminated dark green bituminous shales at the base of the jason Subzone. This Subzone consists mainly of the latter lithology, with some shell beds developed within the shales and at the top of the Subzone.

In the overlying obductum Subzone, thicknesses of shaley clay are developed.

Reference to fig. 49 shows a coincident decrease in the abundance of spore groups with the introduction of the bituminous shale facies at the boundary between the medea and jason Subzones, with a small increase at sample 22, which would support Duff's inferences about the environments of deposition of the shell beds i.e. nuculacean shell beds "are often found at subzonal boundaries, and often contain abundant fragments of wood and bone, suggesting a significant pause in deposition". (1975 p. 467).

Gryphaea shell beds: "Facies associations and consideration of the mode of life of the various infaunal elements, particularly the oysters, suggest that these were deposited in shallower water than the

bulk of the Oxford Clay" (loc. cit. p. 469).

There is a marked increase in the relative percentages of dinoflagellates (i.e. groups 13 - 15) at and above the medea and jason Subzone boundary (sample number 23), with a rapid fluctuation at 22, which corresponds to the increase of the spore groups (1 - 3).

The overall relative frequency of spores at this locality is no higher than at Stewartby (see fig. 50) although at the latter locality we see a marked increase in the thickness of the jason Zone sediments (see fig. 50). Spore and dinoflagellate frequencies apparently fluctuated in cycles throughout the jason Zone and obductum Subzone, which might be a reflection of their response to the fluctuating water levels caused by migrating coastline positions postulated by Duff (1975).

Thus, the establishment of the bituminous shale lithology, which according to Duff marks the onset of the Callovian transgression, occurs at Peterborough from the base of the jason Subzone upward i.e. at the medea/jason boundary.

Stewartby

Bioturbated silts and silty clays comprising the endodatum Subzone pass vertically into the medea sediments, where a basal oyster bed within a silty matrix is overlain by a well laminated olive green clay, similar in lithology to the overlying sediments comprising the jason and obductum Subzones.

Thus the vast majority of the medea Subzone sediments are here developed in the bituminous shale facies, which would apparently indicate the earlier establishment of the facies and, therefore, transgression.

Although there is a slight reduction in spore frequencies seen in

the top half of the medea sediments, and a coincident gradual increase in dinoflagellate abundance, in general, the spore values are equal or higher at this locality and stratigraphic horizon than at Peterborough (particularly groups 1 and 2), where the bituminous shale facies is not established until the medea/jason boundary sediments. The development of the lithology at Stewartby apparently reflects the earlier commencement of the transgression in this region, although the emergent land masses retained their strong influence. A possible explanation might be the proposed form of the London Platform coast line (see pp. 189 and 190).

The bituminous shale facies continues throughout the jason Subzone and basal thicknesses of the obductum Subzone, but towards the top half of this Subzone shell beds occur, some of which are strongly developed, intercalated with shaley bands. The most prominent of these beds is sampled here by specimen 3 (Duff's bed 7, 1975).

At this locality, therefore, we seem to see a combination of a higher spore and lower dinoflagellate frequency than in parts of the succession at Peterborough, and the extensive development of shell beds in the upper half of the obductum Subzone.

Reference to fig. 54 shows that to the east of Stewartby, at Cambridge and Offord Tunnel, there are condensed jason Zone sequences, comprising similar lithologies to the comparable horizons at Peterborough (Beris Cox pers. comm. 1979).

Duff (1975) suggested that "an increase in local current activity during latter parts of the obductum Subzone sequence was responsible for the development of the combination of shell beds, probably on a local swell" (1975 p. 475).

It is here suggested that similar lithological suites could be produced by changes in sea level and, hence, the position of the coast

line with respect to Stewartby, and not only in a response to sea floor topography.

Bletchley

The sediments comprising the endodatum Subzone are recorded by Duff (1975) as very sticky silty clays, with abundant gryphaeate oysters (they were not visible in 1978 being covered by scree deposits) which grade into basal medea silty clays which are bioturbated in part. Lenses of shell beds are intercalated with more well laminated clays rich in molluscs as follows: (where all bed numbers refer to Duff (1975) as shown in fig. 51).

Bed 4C is developed in a shaley facies; 4E in shales and silts and intercalated between the two is an intensely bioturbated horizon - 4D. Beds 5A and 5B and 6 are shell beds in silty clay, 7 and 8 are shaley clay with worm burrows. Only at bed 9, the topmost horizon of the medea Subzone, do we see the introduction of more well laminated shaley clay. At and above the jason/medea Subzone boundary (bed 10 Duff 1975) the bituminous shale facies becomes established and is continuous throughout this and the overlying Subzone, the obductum.

A corresponding sharp drop in spore frequency, and an increase in dinoflagellate abundance, is evident at the top of bed 9 (sample 16) i.e. immediately beneath the jason Subzone lower boundary. This change in the palynological assemblage is apparently coincident with the establishment of the bituminous shale facies. An outline of the palynological assemblages of the beds comprising the medea Subzone seems to suggest an initially fluctuating transgressive period during basal medea times. The moderately high spore levels in samples 22 and 20 are separated by sample 21, containing low spore and high dinoflagellate frequencies. Peaks in spore frequencies approximate

to the worm burrowed horizons and shell beds (samples 17 and 18) and the bioturbated silts (19) concentrated towards the top of the medea sediments. If the establishment of the bituminous shale facies is indicative of the Callovian Transgression i.e. recession of the shoreline (see Duff 1975) which is supported by the palynological results, it would appear to have occurred at a similar time at Bletchley and Peterborough, and slightly later than at Stewartby. The greatest thickness of jason Zone sediments is found at this locality, (see fig. 51).

Calvert

The lowest Subzone exposed here is the jason (Duff 1975 and Callomon 1968) and comprises a basal shell bed, grading upwards into sediments transitional to the shell bed below and the blocky claystone (sensu Duff 1975) above. The sediment identified and named the blocky claystone by Duff in 1975 appears to be unique at this horizon to this locality. Duff records a reduced diversity of bivalve species (Lingula and Solemya are notably characteristic) within a distinctive light grey "plastic" clay. The palynological assemblages for samples of blocky claystone are characterised by high spore and very low dinoflagellate frequencies i.e. samples 15 - 12, with a very marked contrast in the character of the assemblage in sample 11, which is the basal olive green shaley clay (bed 3C, Duff 1975) which overlies the blocky claystone (bed 3B). In contrast to the blocky claystone, this sediment contains a diverse benthonic fauna, which shows a general progressive increase in abundance and diversity upwards (Duff 1975). These sediments are reflected by the abrupt increase in dinoflagellates, Callialasporites and decrease in spore genera and Inaperturopollenites (in sample 11). This sample was taken from just above the termination

of the blocky claystone and the onset of the bituminous shale facies, which is, therefore, a very marked palynological junction.

The thickness of the jason Zone is only slightly reduced from the maximum attained at Bletchley (see fig. 52).

The presence of the 1 metre band of blocky claystone, with its distinctive palynological assemblages and reduced variety of benthos, would seem to indicate that a slightly different environmental situation existed during basal jason Subzone times at this locality. The boundary between beds 3B and 3C have also yielded the only specimen of Metriorhynchus known from this locality (Hudson, Clements, Duff et al unpubl. data 1975). It seems reasonable to argue that these coincidences should be viewed in the light of the environmental control responsible for their occurrence.

Palynological results would appear to indicate that, in the southern East Midlands area, this part of the sequence was laid down slightly closer to land, but where there must have been a high sedimentation rate.

At all the four localities sampled, the obductum Subzone is marked by the presence of shell beds (see figs. 49 - 53). Duff (1975) referring to Brinkmann's (1929) conclusions, argued that this was indicative of a widespread phase of slow deposition i.e. condensed deposition, due to shallowing. In all the localities here sampled, the development of the shell beds is reflected in a rapid increase in spore, Inaperturopollenites and Classopollis frequencies, with a coincident decrease in Callialasporites, dinoflagellates and, to some extent, bisaccates.

Another factor to consider is the decrease in the number and thickness of shell beds as one moves southwards. Duff (1975) draws attention to the shell bed which occurs at, or just above, the base of

the obductum Subzone at Peterborough and Stewartby, but which is absent at Bletchley and Calvert.

Most of the thickness variation occurs within the jason Zone, as shown in fig. 54 , which suggests that conditions were more variable during the deposition of the initial subzones of the Lower Oxford Clay. On the basis of the results outlined here, it would seem that relative proximity to an undulating coastline of the London Platform was controlling deposition, in conjunction with "local configurations of the sea floor" (Duff 1975, p. 472).

RESULTS (5)

PALYNOLOGICAL ANALYSIS OF MATRIX TAKEN FROM MUSEUM SPECIMENS

The matrix adhering to parts of the skeleton of the specimens of Metriorhynchus and Steneosaurus shown in table 29 , was removed and analysed in the same way as samples collected in the field, and the results are presented in a comparable way in fig. 58 and tables 29 - 31 to effect easy comparison of the data. In this way we are comparing palynological results from Norman Cross with those from specimens whose exact locality and stratigraphic horizon are unrecorded. We can, however, from the limited information that is available (see appendix 2), ascertain that all the specimens came from the Peterborough area.

There is a clear disparity between the summed total group values shown in table 31 , between well articulated specimens belonging to the two genera. Placed in the context of the jason Zone values for Norman Cross (Peterborough) in table 25 one might tentatively suggest that the steneosaurs inhabited the Peterborough region at a slightly earlier period i.e. lower levels of the jason Zone, at an earlier phase in the development of the transgression, to be subsequently dominated

by the metriorhynchids at the transgressive maxima within the jason Subzone.

The results obtained from analysis of matrix from the disarticulated bones are more problematical and of dubious significance for two reasons:

1. There is the initial problem of accurate identification of isolated centra, these specimens bearing generic names which had been assigned by a variety of museum curators and workers often with little reason.

2. The problem of transportation away from the niche occupied by the animal, to become part of a transported assemblage which does not bear a close relationship to the environment inhabited. Duff (1975) noted that disarticulated reptilian bones were common elements of shell bed assemblages, which he interpreted as transported assemblages.

RESULTS (6)

COMPARISON BETWEEN BATHONIAN AND CALLOVIAN PALYNOLOGICAL ASSEMBLAGES

The average values of the spore, pollen and dinoflagellates genera counted by Windle (1980) are presented in table 23 . The absolute values are, in the context of this work, not of primary importance, but the general trends which emerge from this data are of considerable interest. They show that "key" genera from the palynological assemblages characteristic of the sediments comprising the basal and topmost levels of the succession at Peterborough, Stewartby and Calvert, and the topmost strata at Bletchley (distinguished above as groups 1 and 2), show relative percentages which either intermediate between Windle's groups 1 and 2, or approximate to his group 1.

It seems that we are seeing the palynological expression of an overlap in the range of environments between the Bathonian and Lower

Oxford Clay i.e. Callovian, where the "most marine" environment sampled in the Bathonian is largely comparable to the one reflected by the groups 1 and 2 in the present study for the Callovian. Nowhere in the Callovian are assemblages encountered which show the values characteristic of Windle's lagoonal or terrestrial environments (i.e. his groups 3 and 4) or, for that matter, of Muir's coal swamp or non-marine shale and siltstone facies (1964). The present analysis has shown an extension of Windle's range of environments to incorporate the depositional environments which produced the majority of the jason Zone and obductum Subzone sediments in the East Midlands.

DISCUSSION

In results (4), Duff's (1975) sedimentological and invertebrate faunal assemblage data and the palynological analysis completed for the present work were compared. This comparison can also be viewed in the wider context of Woollam's Lower Oxford Clay results (1977) for the East Midlands, Yorkshire and Dorset and Callovian presence, thickness and facies in the surrounding districts of Yorkshire and the southern North Sea, so that by combining these data we can try to determine the extent to which the environment controlled the distribution of the crocodiles.

Fig. 59a (taken from part of fig. 15a, Woollam 1977) illustrates the level of detail of sampling by Woollam and the geographic locality, in the zones of the Oxford Clay relevant to the present work. Samples 1 - 4 are particularly relevant. The results of the spore/plankton count for these samples are shown in fig. 59b , which give an outline of the relative percentage of miospores to plankton, and the variation seen in this relationship in the four samples which span

the medea, jason and obductum Subzones at Stewartby. The peak for the plankton corresponds to the jason Subzone sample, which agrees with the more detailed results obtained from the present work (see tables 19 - 22). If one accepts that this increase in the percentage of microplankton reflects the transgression at the base of the Middle Callovian, Woollams' work lends support to the concept argued by Duff (1975), and supported by the results outlined in this work, that the jason and obductum sediments represent "a cycle of environmental conditions ..... a deepening, transgressive sequence from the Kellaways Rock through the transition beds into the bituminous shales of the jason/obductum Subzones, with indications of shallowing towards the top" (Duff 1975, p. 475).

Hallam (1967a, p. 489) suggested that bituminous shale deposition was often widespread and characteristic or indicative of conditions near to the base of transgressive sequences, arguing that this phase was followed by more fossiliferous, deeper water clays and shales. Duff (1975) referring to Hallam's model, notes that, in general, the East Midlands Lower Oxford Clay sequence - Kellaways Rock to bituminous shales, which comprise the bulk of the Lower Oxford Clay, agrees with his model, where the medea, jason and obductum Subzones represent the bituminous shale part of the cycle.

The Yorkshire Callovian sediments have been described in detail by Wright (1968), who described and compared the succession at Peckondale Hill, Malton and in the Scarborough district, Yorkshire (see fig. 60) in two papers in 1968, with the generalised succession in central and southern England as shown in fig. 60.

At Malton the Lower Callovian calloviense Zone consists of 30 feet of feldspathic sandstone: the Kellaways Rock. These sandstones are overlain unconformably by 30 feet of lower coronatum Zone sediments,

developed in a shaley clay facies, which are overlain unconformably by Upper Callovian clays, with a minimum thickness of 35 feet (Wright 1968a i.e. 15 feet athleta and a minimum of 20 feet of lamberti Zone sediments.

At Scarborough the calloviense Zone is developed in a sandstone and ironstone facies to a thickness of 30 feet: the Kellaways Rock (whose age was established as lower calloviense by Wright in 1968(a). This is overlain unconformably by 35 feet of sandstone. Wright established the age of these beds as Middle Callovian - upper coronatum age. They comprise medium grained marine sandstones, with a scarce ammonite and stunted lammellibranch fauna, noted by Wright to be similar to those formed close to beaches where the energy of the waves is sufficient to transport sand grains of that size. He termed these the "Langdale Beds". In the west of the Scarborough region the Langdale Beds comprised medium grained excellently sorted, current bedded sandstones. Progression eastwards was accompanied by a gradual decrease in the degree of sorting and grain size, and an increase in the occurrence of ammonites, which Wright argued to be indicative of an increase in water depth and, presumably, distance from shoreline.

The Langdale Beds are succeeded, again unconformably, by a condensed sequence of calcareous, chamositic sandstones and sandy oolites comprising the Hackness Rock of Upper Callovian age (Wright 1968b), spanning the athleta and lamberti Zones, 4 feet 3 inches and 2 feet in thickness respectively (the lamberti thickness being equivalent to 50 - 100 feet of Middle Oxford Clay in southern England).

Wright's comparison of the Callovian succession at these Yorkshire localities illustrates clearly that the uplifts that affected the Scarborough district during Middle Callovian times (resulting in the unconformable relationships between coronatum and calloviense sediments)

also affected the Malton area. There are, however, distinct differences between the timing of the uplifts and the facies of the Callovian sediments at these localities, to which Wright draws attention. Middle Callovian sediments present in the Malton area are of Lower coronatum age, and the grossouvrei Subzone (represented by 35 feet of Langdale Beds in the Scarborough district) is unrepresented here. At Malton, beds of athleta and lamberti age are developed in shale/clay facies with no sign of the "Hackness Rock facies", as developed at Scarborough.

Thus, in Middle and Upper Oxford Clay times, Wright concluded there to have been a link between the Malton Oxford Clay and that of central and southern England reflected in the similar facies development in these two regions (see fig. 60). He decided that the Market Weighton Axis "had no influence on the distribution of the clay - Hackness Rock facies in the Middle and Upper Callovian of the Yorkshire Basin" (1968 (a) p. 96) and argued that his results supported Brinkmann's conclusion (1926) that the Callovian succession at Scarborough seemed to have been deposited close to the margin of the Callovian sedimentary basin as reflected in the facies and non-sequences comprising the succession. Wright concluded that the Peckondale Hill succession was "intermediate, being of the same facies as the Oxford Clay of central and southern England, but having the non-sequences typical of the Scarborough district" (1968 (a) p. 96).

His observations thus provided detailed evidence for the presence of a coastline and, therefore, emergent land mass in the proximity of Scarborough, agreed by later authors (e.g. Hallam & Sellwood (1975) in the JNSS Symposium).

Fig. 61 (a) (after Woollam 1977) indicates that, in the Lower and Middle Callovian in Yorkshire and the East Midlands, palynological

assemblages show high proportions of miospores. It is known that the relative proportions of miospores to microplankton are a result of the distance of a locality from a major land mass. These assemblages would seem to indicate, therefore, the widespread emergence of land masses in these regions at this time.

In the Upper Callovian (Lower Oxfordian in Yorkshire), assemblages in the East Midlands and Yorkshire maintain high levels of miospores (see fig. 61 (b) and (c)) in contrast to assemblages from Dorset and Normandy shown in the same figure, (Woollam 1977). He argued that this was consistent with localised, continued emergence of land masses in the East Midlands and to the north in Yorkshire. He attributed the variation in proportions of microplankton to miospores to the response to "the varying proximity of the shore effected by transgression and regression" (1977 p. 114).

Jurassic North Sea sediments extend in a north - south trending belt in the Viking (to the north) and Central Grabens, being broadly delimited in the west by the structural highs of the east Shetland Platform and the Mid North Sea High respectively. In the context of this study, only the most south-western extremities of the Mid North Sea High are of relevance, and might possibly have influenced the overall environment of the East Midlands, (see fig. 62). The Callovian and Oxfordian stages in the Southern North Sea Basin (see fig. 62) are more widespread than the underlying early Middle Jurassic fluvial and deltaic sandstones and intercalated non-marine shales and coals. The lithologies of the lowest Callovian Southern North Sea sediments reflect the onset of the marine transgression witnessed throughout the East Midlands and southern England, and comprise marine, mainly argillaceous sediments. Their continued absence on the southern end of the Mid North Sea High, however, deliniates the extent of this

emergent land mass during the Lower and Middle Callovian.

On the basis of the Callovian successions outlined in this section (their facies, thickness and presence of non-sequences and their spatial relationships with each other, and the detailed palynological and sedimentological comparisons in Results (4)) a palaeogeography for the Middle Callovian is outlined in fig. . This is a composite figure, based on data from Gallvis & Cox (1977), JNSS Symposium (1975), Woollam (1977), Duff (1975) and Wright (1968) and where the modifications to the London Platform coastline is based on data collected in the present work.

The Palaeoecology of the Bathonian steneosaurs

Windle (1980) sampled the Hampton Marley and Sharps Hill formations which occur beneath the White Limestone and the Fimbriata-Waltoni Clay which immediately overlies, and is separated by a plane of erosion from (Arkell 1931), the White Limestone. These three stratigraphic horizons reflect in their lithologies three regressive cycles in the Bathonian, separated by the marine White Limestone. This is an oolitic fine grained limestone representative of "widespread shallow water carbonate sedimentation" (Palmer & Jenkyns 1975 p. 125). Within the Fimbriata-Waltoni Clay, a cyclic series of marine clays with lenses of shelly limestone with a fully marine fauna, through brackish water clays with a restricted lammelibranch fauna indicative of reduced salinity and fresh water ostracods, to marine clays, reflect minor transgressive and regressive cycles.

Arkell (1931) recorded the presence of abundant lignite, and reptilian bones from these horizons, including the remains of Ceteosaurus, and it seems likely that it is in these beds, perhaps from the intercalated shelly limestones, at the very top of the White Limestone, that

the Steneosaurus remains described by Phizackerley (1951) were located. Crocodile bones have been observed in the field at this horizon by Windle (1980 pers. comm.). It should be noted, however, that some of the matrix adhering to the steneosaur skulls in the Oxford University Museum seems too pure a limestone to be associated with the Fimbriata-Waltoni Clay, and is more likely to have come from the beds that immediately underlie them.

Palmer & Jenkyns (1975) investigated facies development in the upper formations of the Great Oolite Group (Bathonian) in the Oxfordshire district: the White Limestone and the Forest Marble.

Previous workers had variously interpreted these formations (on the basis of the sedimentary evidence) to be the product of subtidal and intertidal environments (Klein 1963, 1965) (M^{c}Kerrow, Johnson & Jakobson 1969) and, therefore, "Implicitly recognised the proximity of emergent areas in this part of the Bathonian shelf sea" (Palmer & Jenkyns p. 125).

Palmer & Jenkyns mapped the extent of what they believed to be the best indicator of emergence in an area north of Oxford, which was a bed of algal laminated vuggy micrite. This lithology was developed locally at the top of the White Limestone. It was composed of an unfossiliferous calcite micrite, with sedimentary structures including: ellipsoidal vugs, anastomosing cracks, vertically orientated tubular cavities, laminae, V shaped cracks - wedging out downwards and delineating polygons in horizontal section, and polygonal micrite flakes (Palmer & Jenkyns 1975). The vugs and cracks were ascribed by these authors to desiccation and shrinkage in a supratidal environment. The polygons deliniated by the wedges showed the characters which typified mud cracks formed by subaerial desiccation. The laminae were interpreted as being stromatolitic in origin. They argued that these structures collectively indicated a high intertidal -

supratidal zone (the environmental significance of this lithology being indicated by its close similarity to Recent lime muds comprising mud flat islands in Florida bay).

Towards the top of the White Limestone formation, Palmer & Jenkyns detected many lateral facies equivalents in their area of study and, in the area shown in fig. 63 (after Palmer & Jenkyns 1975 figs. 3 and 4), deposition of the White Limestone culminated in the deposition of the laminated micrite in a north west - south east trending belt. At the equivalent horizon to the south west, the facies is one of cross-bedded oopelsparites with shell debris where the tops of the cross-bedded units i.e. the top-set and fore-set beds, are commonly developed as burrowed hardgrounds. At the localities E T U V W (see fig. 63) the lateral equivalent of the laminated micrite is a shelly micrite underlain by two metres of clays - the Fimbriata-Waltoni Clay (Arkell 1931), and it is these sediments that were sampled by Windle (1980).

Palmer & Jenkyns (1975) do not present any detailed quarry sections which could define the north and eastern limits of the extent of the laminated micrite, which they termed the "emersion horizon". They apparently based their conclusions about the palaeogeographic significance of the spatial relationship between the lithological suites they mapped, on the detail of two sections D and C which characterise the development of the emersion horizon, and its associated lithologies, with two sections to the north A and B and four to the south H - E. By comparing the lithologies developed at A and B and H - E in the Forest Marble they deduced that the regionally varied and irregularly distributed environments of deposition prevailing towards the end of White Limestone times, i.e. shallow marine and brackish water and emergent areas, developed into two markedly contrasted depositional environments during Forest Marble times, due to their separation by a

carbonate barrier. At A and B the Forest Marble is developed in low salinity clays with abundant lignite and in situ rootlets. At H - E the Forest Marble is developed as fully marine cross-bedded oobiosparites with thin clay intercalations. Their palaeogeographic reconstruction is reproduced here in fig. 64 (after Palmer & Jenkyns 1975 p. 132, fig. 6).

Locality E i.e. Greenhill Quarry is of most relevance because it is close to the localities and stratigraphic levels from which steneosaurs were recorded by Phizackerley, the sedimentology of the sequence is shown in detail by Palmer & Jenkyns, and the Fimbriata-Waltoni Clays from this region have been sampled by Windle, and palynological results from this facies are reproduced here (from Windle's data (1980)).

If one accepts Palmer & Jenkyns' palaeogeographic interpretation, locality E is extremely close to the proposed southern boundary of the carbonate barrier. Palmer & Jenkyns' interpretation hinges on establishing that the Fimbriata-Waltoni Clays and rootlet bearing clays (which they call the Forest Marble) are not synchronous deposits i.e. laterally equivalent beds.

Windle (1980 pers. comm.) does not agree with Palmer & Jenkyns' correlation between sections and, on the basis of evidence contained in his thesis, would place the Fimbriata-Waltoni Clays additionally at the base of the Forest Marble.

Although the chronological relationship between the carbonate and various clay facies may be problematical, the occurrence of these lithologies and their associated faunas, floras and sedimentary structures, and the context of the succession in which they occur, are certainly indicative of a major regressive phase which occurred in late White Limestone - Early Forest Marble times in this region.

Regardless of the interpretation one chooses, the association of

crocodilian remains with these lithologies gives an indication of the type of environment that these crocodiles inhabited i.e. fluctuating between shallow marine to supratidal and lagoonal conditions, certainly in reasonable proximity to the coastline of the London Platform and possibly in close proximity to the island barrier proposed by Palmer & Jenkyns (1975).

CONCLUDING STATEMENTS

The object of this chapter has been to attempt to explain the distribution of the Callovian Crocodiles in relation to their environment. To this end, a palaeogeographic reconstruction of the East Midlands during Middle Callovian times has been attempted, and is illustrated in fig. 54 . Some modifications to the currently accepted form of the coastline of the London Platform are proposed, based on the following lines of evidence:

1. Borehole and outcrop thicknesses of jason Zone sediments in the area embracing Cambridge, Upwood, Warboys, Offord Tunnel, Denver and Peterborough, show that the sequences are condensed at these localities.

2. There are higher spore to plankton ratios at Peterborough and Stewartby than at Bletchley and Calvert.

3. There is a high concentration in the development of shell beds in the Peterborough succession (Duff 1975).

4. The presence of dinosaur bones is exclusive to the Peterborough region (C. A. Walker pers. comm. 1980).

5. The concentration of crocodiles is virtually exclusive to the Peterborough area. The only other known crocodilian material comprises an isolated section of mandible from Bletchley (Callomon pers. comm. 1978) and a single, reasonably well articulated Metriorhynchus skeleton from Calvert.

It is suggested that these facts can be explained by the presence of an undulation of the London Platform coastline, as shown in fig. 54 near Peterborough, Denver, Upwood, Offord Tunnel and Cambridge during jason Zone times.

Thus, borehole and outcrop jason Zone thicknesses show that to the north and east of Stewartby there existed, at this time, an area of condensed deposition, while Stewartby apparently characterised an area which was "intermediate" between Bletchley and Calvert - illustrated by the intermediate thickness of jason Zone sediments, their palynological content and the development of shell beds in the jason and obductum Subzones at this locality. There are marked increases in jason Zone thicknesses at Bletchley, Calvert and Milton Keynes.

In conjunction with lower spore frequences at Bletchley and Calvert and the virtual absence of crocodiles, the ichthyosaurs and plesiosaurs increase markedly in abundance in Bedfordshire and Buckinghamshire to become the dominant elements of the vertebrate fauna (pers. comm. Delair 1978). There is a coincident decrease in the development of shell beds at these localities (Duff 1975).

It seems that the above pattern of sedimentation and the floral and faunal content of the sediments, is a reflection of the interreaction between the proximity to land of the localities analysed, and the topography of the sea floor. In this region the area of condensed sedimentation suggests a "shelf sea" region near the proposed undulation of the London Platform coastline. The two most southerly localities here sampled i.e. Bletchley and Calvert represent deposition in more open, and possibly deeper, marine conditions - further offshore. This pattern of depositional environments apparently controlled the vertebrate faunal provinces which are strongly indicated in the East Midlands (see above).

At Bletchley, the palynological analysis has indicated a fluctuating initiation to the Callovian transgression, where the fluctuating sea level (which determines the position of the shoreline) is evidenced in the vertical series of lithologies and their palynological assemblages (see pp.175, 176 and fig. 51).

At Calvert we see evidence, during jason Subzone times, for the existence of a unique environmental control, which produced the Blocky Claystone facies (Duff 1975). The isolated occurrence of a single Metriorhynchus and a very distinctive palynological assemblage in these sediments, correlate with this unique lithology. It seems that a unique, but very localised, environmental situation prevailed here at this time.

In a wider palaeogeographical context, the presence of landmasses bordering the Southern North Sea basin, and in Yorkshire and Cheshire (see fig. 62) extending as far south as the North Midlands, South Yorkshire and Derbyshire, in conjunction with the London Platform, were instrumental in producing a sheltered, continental, shallow marine environment.

The crocodile population apparently inhabited the marine area closest to these northern landmasses, although the degree of influence exerted by these landmasses over the "micro-environment" at Peterborough remains difficult to estimate.

The brick pits concentrated in the Peterborough region were the only outcrops in the suggested shelf sea area around Cambridge and Denver etc. from which detailed collections were made by the Leeds brothers, and for which detailed palynological and sedimentological analysis for the jason Zone can be carried out.

It seems most likely that the proposed undulation of the London Platform coastline in the Peterborough region provided a near-shore,

shelf sea, environment - with reasonably shallow and sheltered waters, and localised potential breeding sites, which the Callovian Crocodiles occupied.

The more southerly localities here sampled were further offshore, away from the influence of the westward undulation and were, presumably, exposed to more open marine conditions with attendant wave and current action and fewer potential breeding sites.

The results of the analysis of the "museum matrix" would suggest that, although a degree of niche disparity existed between the stenosaurs and metriorhynchids, it was much less than the currently accepted situation. There is no evidence to support the theory that the Callovian steneosaurs occupied the coastal or beach province i.e. that both genera were fully marine (although this might well have been the case for the Bathonian steneosaurs).

The osteological evidence presented in chapter two suggested that the steneosaurs were slower swimmers, and they might well have favoured slightly more near-shore, sheltered and calmer waters without strong currents and waves.

The isolated crocodile skeleton recovered from Calvert belongs to the genus Metriorhynchus, which is here suggested to have been able to swim more rapidly than Steneosaurus, and to have coped more readily with offshore marine currents.

It is possible that as the interval between the onset of the Callovian transgression at Peterborough progressively increased (i.e. at successively higher levels in the jason Zone), and the coastline migrated eastwards, the steneosaurs were replaced by the more abundant metriorhynchids. This theory is supported by the similarity between the character of the palynological assemblages obtained from matrix attached to articulated steneosaurs and topmost endodatum and basal

medea Subzone assemblages from the field at Peterborough, and the correlation between the assemblages characterising the upper *medea* and *jason* Subzone sediments at Peterborough and matrix attached to metriorhynchid specimens.

Thus it has been possible to produce a *jason* Zone palaeogeography based on the overall spatial relationships between the thickness and floral and faunal content of the *jason* Zone sediments in the entire region. This must have (in the first instance) determined the region which the crocodiles inhabited.

It has also been possible to look further at the *jason* Zone sediments at each locality in a vertical sense, to analyse the detailed changes in the depositional environment with time within this generalised palaeogeography.

An attempt has been made to correlate the vertical series of lithologies and palynological assemblages in the *jason* Zone at Peterborough, with the role of the changing environmental conditions in controlling the distribution, with time, of the two genera of crocodiles, shown by the Leeds Collection, to exist at that locality.

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APPENDIX 1

I. CRANIAL MEASUREMENTS FOR STENEOSAURUS AND METRIORHYNCHUS

II. CRANIAL CHARACTERS IN STENEOSAURUS AND METRIORHYNCHUS

III. MULTIVARIATE COMPUTER SHEETS

A i

B i - ii

C i

D i - iii

E i - ii

F i - ii

TABLE 32

CRANIAL MEASUREMENTS IN STENEOSAURUS	B.M.(N.H.) R 3320	R 3806	R 2619	R 2074	R 3701	R 2865	R 3168	O.U.M. R 2617	J 1401
Total length of skull	810	853		600	740	935	1160	1000	768*
Length of s.t.fenestrae	120	142		153	180	225	299	140	
Preorbital length	590	613		350	450	589	710	730	474
Width at outer angles of quadrates	180	204		220	240	312	375	250	
Width of s.t.fenestrae	73	82		80	88	98	140	105	
Width of snout at anterior end of nasals	43	59		54	64	82	90	63	58
Width of skull at anterior rim of orbits	105	125		107	114		189	167	134*
Distance between nasals and premaxillae	264	272		148	192	280		455	
Mandible length	890	960	790	720	850		1370	1100	
Length of symphysis	520	508	431	289	375		580	620	
Long diameter:orbits	55			53					70
Transverse diameter: orbits	37			41					49

N.B. All measurements in mms.

* Estimated value.

TABLE 32 (contd.)

CRANIAL MEASUREMENTS IN STENEOSAURUS	J1403	J29850	J29851	J1420	H.M.(U.G.)	v1150 C.M.P.	R179	R175	R178	S.M. 1
Total length of skull	820*	746	731	792	744	598	1112	1030*	1003	
Length of s.t.fenestrae	203	183	158	156	135	118*	249	255	140	
Preorbital length	508	474	464	509	533	378	686	635	752	
Width at outer angles of quadrates	264	232	240	212	181	175	312	348	234	
Width of s.t.fenestrae	102	72	72*	71	63	49	118	119	96	
Width of snout at anterior end of nasals	66	53	51	48	48	43	82	81	58	
Width of skull at anterior rim of orbits	153	104	119	113	112	92	156	192	134	
Distance between nasals and premaxillae	201	253	265	220	294	201	388	232	397	
Mandible length		856								
Length of symphysis		407		418*		328	590*			
Long diameter:orbits	72	60	68	60	44	35*	55	67		
Transverse diameter: orbits	52	45	45	36	33	26	42	52		

TABLE 33

CRANIAL MEASUREMENTS IN MEIRIORHYNCHUS

	B.M.(N.H.)	R3015	R3014	R4762	R2031	R3899	R 3540	R2054	R2044	R2053
Length in mid-dorsal line		480	450					607	575	
Length from occ.condyle to tip of snout	315			295*	375*	340*	405	372	295	
Length of frontal, anterior to s.t.f.	82		75	79	85	93	78	91	70	
Distance between nasals and premaxillae	100	95	80	90	100*	85	74	60	45	
Length of nasals	150	135*		163	194	200	243	225	180	
Length of s.t.crest	83						124	112		
Least width between the orbits	54	40*	40	57	77	95	84	89	60	
Width between outer angles of prefrontals	114	90*	111	109	138	146	148	130	107	
Width between outer angles of quadrates				133	180	178	185			
Mandible length		492					720	635		
Length of symphysis							360	270		

s.t.f. supratemporal fenestrae

TABLE 33 (contd.)

CRANIAL MEASUREMENTS IN METRIORHYNCHUS	R2030	R2058	R2051	R2041	R2055	R2032	R3804	R3541
Length in mid-dorsal line	634	600	510	522	480*	595	738	
Length from occ.condyle to tip of snout	660		555	552			772	
Length from anterior end of frontal to tip of snout	275						407	304
Length of frontal, anterior to s.t.f.	65					80	143	105
Distance between nasals and premaxillae	90	75	55	55	70	79	58	38
Length of nasals	213		200	195	170	206	252	195
Length of s.t.crest							179	
Least width between the orbits	50	81	82	71	67	64	80	123	88
Width between outer angles of prefrontals	92	150	130	117	114	114		255	166
Width between outer angles of quadrates		185			156	135		254	
Mandible length		720			560		670	823	
Length of symphysis	175	305					270		

TABLE 33 (contd.)

CRANIAL MEASUREMENTS IN METRIORHYNCHUS	R3700	R3699	R3939	R3321	R2039	R2618	H M (U.G.)	v962	v963	v964
Length in mid-dorsal line	615	635				425				560
Length from occ.condyle to tip of snout	680	700								594
Length from anterior end of frontal to tip of snout	380*	392				238	366			355
Length of frontal, anterior to s.t.f.	110	128	145	109	112	80	91	53		90
Distance between nasals and premaxillae	0	16		18	25	26	106	89		
Length of nasals	250	247		196	187	148	216			205*
Length of s.t.crest									78	121
Least width between the orbits	104	105	126	119	127	72	69		46	87
Width between outer angles of prefrontals	213	224	233	229	229	149	140*		85	134
Width between outer angles of quadrates		247							104	172
Mandible length										
Length of symphysis										

TABLE 33 (contd.)

CRANIAL MEASUREMENTS IN METRIORHYNCHUS	v965	v966	v971	v973	v975	v978	v981	v982	v983
Length in mid-dorsal line	575*	550*	589			494*			
Length from occ.condyle to tip of snout	615*	583*	639			529*			
Length from anterior end of frontal to tip of snout	374	350	385			300*			
Length of frontal, anterior to s.t.f	84	87	84	87		98	84		88
Distance between nasals and premaxillae	98	62	81			78		72	
Length of nasals	213	169	253	206*		206			
Length of s.t.crest	115	122	114	117	109	99	118		98
Least width between the orbits	78	90	77	76*	76	84	73	79	79
Width between outer angles of prefrontals	132	136	148	130*	141	150*	129	134	129
Width between outer angles of quadrates		166*	186	188	183	167	170*	172	166*
Mandible length									
Length of symphysis									

TABLE 33 (contd.)

CRANIAL MEASUREMENTS IN METRIORHYNCHUS	v985	v987	v989	v998	v1015	v1140	v1142	v1143	v1004
Length in mid-dorsal line	599	632		563	590*	619	576	595	680*
Length from occ.condyle to tip of snout	631	671		591		657	614		735
Length from anterior end of frontal to tip of snout	374	412	335*	359*	380*	403	384	408	
length of frontal, anterior to s.t.f.	103	91	91	88	79	98	85	76	
Distance between nasals and premaxillae	77	50	93	89*	73	84	65	132	
Length of nasals	232	256	189	206	255	222	214	184	
Length of s.t.crest	119	124		108	120*	121	106	103	128
Least width between the orbits	88	92	61	77	78	74	74	80*	92
Width between outer angles of prefrontals	145	156	112	133	132	139	129	134*	156
Width between outer angles of quadrates	197	204				197	166	177	206*
Mandible length								636	
Length of symphysis								294	

TABLE 33 (contd.)

CRANIAL MEASUREMENTS IN METRIORHYNCHUS	v1000	L54498/1 C.M.P.	R176	R19	R24	R8	R10	R17	R42
Length in mid-dorsal line			802						
Length from occ.condyle to tip of snout			853						
Length from anterior end of frontal to tip of snout			506			418			
Length of frontal, anterior to s.t.f.	96		130	114	82		92		99
Distance between nasals and premaxillae	89		33				71	84	79
Length of nasals	242	260	339*		187		247	229	198
Length of s.t.crest	85		166	120		113			127
Least width between the orbits	100	95	111	91		72	79		85
Width between outer angles of prefrontals	152	174	208	206	122	126	152	164	140
Width between outer angles of quadrates	198	232	283	256	153	165	181		
Mandible length									
Length of symphysis									

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TABLE 33 (contd.)

CRANIAL MEASUREMENTS IN METRIORHYNCHUS	R180	R18	R20	N.M.W.	C179	S.M.	A	B	C
Length in mid-dorsal line			530*	600*	596				
Length from occ.condyle to tip of snout			572*	638*	624				
Length from anterior end of frontal to tip of snout			322*	370*	406	238	373		
Length of frontal, anterior to s.t.f.	58	91	97	114	82	71	102		
Distance between nasals and premaxillae	58	79	97	84	34	119			
Length of nasals		233	218	178	174	154	216		
Length of s.t.crest	67		111	120	108		117		
Least width between the orbits	41	79	78	77	79	47	83		
Width between outer angles of prefrontals	81	138	128*	147	139	89	151		
Width between outer angles of quadrates	94		189	206	172				
Mandible length									
Length of symphysis									

APPENDIX 1

STENEOSAURUS

CHARACTER 1

Preorbital region as a % of total length of the skull

(all measurements in mms)

S. leedsi	Total length	Preorbital length	%
B.M.(N.H.)			
R3320	810	590	72.83
R3806	853	613	71.86
H.M.(U.G.)			
v1150	744	533	71.63
C.M.P.			
R179	598	378	63.21
S. hulkei			
B.M.(N.H.)			
R2074	600	350	58.33
S. durobrivensis			
B.M.(N.H.)			
R3701	740	450	60.81
R2865	935	589	62.99
C.M.P.			
R175	1112	686	61.69
S. obtusidens			
B.M.(N.H.)			
R3168	1160	710	61.20
C.M.P.			
R178	1030 e	635	61.65

M. nasutus			%
B.M.(N.H.)			
R2617	1000	730	73.00
S.M.			
1	1003	752	74.90
S. boutilieri			
O.U.M.			
J1401	768	474	61.71
J1403	820	508	61.95
S. meretrix			
O.U.M.			
J29850	746	474	63.53
J29851	731	464	63.47
S. depressus			
O.U.M.			
J1420	792	509	64.26

CHARACTER 2

Ratio of width of skull to total length of skull

	Skull length	Skull width(quadrates)	
S. leedsi			
B.M.(N.H.)			
R3320	810	180	4.5 : 1
R3806	853	204	4.18: 1
H.M.(U.G.)			
v1150	744	181	4.11: 1
C.M.P.			
R179	598	175	3.41: 1

S. hulkei			
B.M.(N.H.)			
R2074	600	220	2.72: 1
S. durobrivensis			
B.M.(N.H.)			
R3701	740	240	3.08: 1
R2865	935	312	2.99: 1
C.M.P.			
R175	1112	312	3.56: 1
S. obtusidens			
B.M.(N.H.)			
R3168	1160	375	3.09: 1
C.M.P.			
R178	1030	348	2.95: 1
M. nasutus			
B.M.(N.H.)			
R2617	1000	250	4.0 : 1
S.M.			
1	1003	234	4.28: 1
S. boutilieri			
O.U.M.			
J1403	820	264	3.1 : 1
S. meretrix			
O.U.M.			
J29850	746	232	3.21: 1
J29851	731	240	3.04: 1
S. depressus			
O.U.M.			
J1420	792	212	3.73: 1

CHARACTER 3

Length of temporal fenestrae as a % of total length of the skull

S. leedsi	Total length	Length of fenestrae	%
B.M.(N.H.)			
R3320	810	120	14.81
R3806	853	142	16.64
H.M.(U.G.)			
v1150	744	135	18.14
C.M.P.			
R179	598	118 e	19.73
S. hulkei			
B.M.(N.H.)			
R2074	600	153	25.50
S. durobrivensis			
B.M.(N.H.)			
R3701	740	180	24.32
R2865	935	225	24.06
C.M.P.			
R175	1112	249	22.39
S. obtusidens			
B.M.(N.H.)			
R3168	1160	299	25.70
C.M.P.			
R178	1030 e	255	24.75
M. nasutus			
B.M.(N.H.)			
R2617	1000	140	14.00
S.M.			
1	1003	140	13.95

S. boutilieri			%
O.U.M.			
J1403	820	203	24.75
S. meretrix			
O.U.M.			
J29850	746	183	24.53
J29851	731	158	21.61
S. depressus			
O.U.M.			
J1420	792	156	19.69

CHARACTER 4

Length of the supratemporal fenestrae as a % of preorbital length

S. leedsi	Preorbital length	Length of fenestrae	%
B.M.(N.H.)			
R3320	590	120	20.33
R3806	613	142	23.16
H.M.(U.G.)			
v1150	533	135	25.32
C.M.P.			
R179	378	118 e	31.21
S. hulkei			
B.M.(N.H.)			
R2074	350	153	43.71
S. durobrivensis			
B.M.(N.H.)			
R3701	450	180	40.00
R2865	589	225	38.20
C.M.P.			
R175	686	249	36.29

S. obtusidens			
B.M.(N.H.)			
R3168	710	299	46.47
C.M.P.			
R178	635	255	40.15
M. nasutus			
B.M.(N.H.)			
R2617	730	140	19.17
S.M.			
1	752	140	18.61
S. boutilieri			
O.U.M.			
J1403	508	203	39.96
S. meretrix			
O.U.M.			
J29850	474	183	38.60
J29851	464	158	34.05
S. depressus			
O.U.M.			
J1420	509	156	30.64

CHARACTER 5

The width of the temporal fenestrae as a % of the width at the outer angles of the quadrates

S. leedsi	Skull width(quadrates)	Width of fenestrae	%
B.M.(N.H.)			
R3320	180	73	40.55
R3806	204	82	40.19

S. leedsi (contd.)			%
H.M.(U.G.)			
v1150	181	63	34.80
C.M.P.			
R179	175	64	36.57
S. hulkei			
B.M.(N.H.)			
R2074	220	80	36.36
S. durobrivensis			
B.M.(N.H.)			
R3701	240	88	36.66
R2865	312	98	31.41
C.M.P.			
R175	312	118	37.82
S. obtusidens			
B.M.(N.H.)			
R3168	375	140	37.33
C.M.P.			
R178	348	119	34.19
M. nasutus			
B.M.(N.H.)			
R2617	250	105	42.00
S.M.			
1	234	96	41.00
S. boutilieri			
O.U.M.			
J1403	264	102	38.63

S. meretrix			%
O.U.M.			
J29850	232	72	31.03
J29851	240	72	30.00
S. depressus			
O.U.M.			
J1420	212	71	33.49

CHARACTER 6

Width of the snout at the anterior end of the nasals as a % of preorbital length

S. leedsi	Preorbital length	Width of snout	%
B.M.(N.H.)			
R3320	590	43	7.28
R3806	613	59	9.62
H.M.(U.G.)			
v1150	533	48	9.00
C.M.P.			
R179	378	43	11.37
S. hulkei			
B.M.(N.H.)			
R2074	350	54	15.42
S. durobrivensis			
B.M.(N.H.)			
R3701	450	64	14.22
R2865	589	82	13.92
C.M.P.			
R175	686	82	11.95

S. obtusidens			%
B.M.(N.H.)			
R3168	710	90	12.67
C.M.P.			
R178	635	81	12.75
M. nasutus			
B.M.(N.H.)			
R2617	730	63	8.63
S.M.			
1	752	58	7.71
S. boutilieri			
O.U.M.			
J1403	508	66	12.99
S. meretrix			
O.U.M.			
J29850	474	53	11.18
J29851	464	51	10.99
S. depressus			
O.U.M.			
J1420	509	48	9.43

CHARACTER 7

Width of the skull opposite the anterior rim of the orbits, as a % of preorbital length

S. leedsi	Preorbital length	Width of skull	%
B.M.(N.H.)			
R3320	590	105	17.79
R3806	613	125	20.39

			%
S. leedsi (contd.)			
H.M.(U.G.)			
v1150	533	112	21.00
C.M.P.			
R179	378	92	24.33
S. hulkei			
B.M.(N.H.)			
R2074	350	107	30.57
S. durobrivensis			
B.M.(N.H.)			
R3701	450	114	25.33
C.M.P.			
R175	686	156	22.74
S. obtusidens			
B.M.(N.H.)			
R3168	710	189	26.61
C.M.P.			
R178	635	192	30.23
M. nasutus			
B.M.(N.H.)			
R2617	730	167	22.87
S.M.			
1	752	134	17.81
S. boutilieri			
O.U.M.			
J1401	474	134	28.27
J1403	508	153	30.11

S. meretrix			%
O.U.M.			
J29850	474	104	21.94
J29851	464	119	25.64
S. depressus			
O.U.M.			
J1420	509	113	22.20

CHARACTER 8

Distance between the premaxillae and nasals as a % of the length of the rostrum

S. leedsi	Length of rostrum	Distance:premax./nasals	%
B.M.(N.H.)			
R3320	590	264	44.74
C.M.P.			
R179	378	201	53.17
H.M.(U.G.)			
v1150	533	294	55.15
S. hulkei			
B.M.(N.H.)			
R2074	350	148	42.28
S. durobrivensis			
B.M.(N.H.)			
R3701	450	192	42.66
R2865	589	280	47.53
C.M.P.			
R175	686	388	56.55
S. obtusidens			
C.M.P.			
R178	635	232	36.53

			%
M. nasutus			
B.M.(N.H.)			
R2617	730	455	62.32
S.M.			
1	752	397	52.79
S. boutilieri			
O.U.M.			
J1403	508	201	39.56
S. meretrix			
O.U.M.			
J29850	474	253	53.37
J29851	464	265	57.11
S. depressus			
O.U.M.			
J1420	509	220	43.22

METRIORHYNCHUS

CHARACTER 1

Width between the outer angles of the quadrates in relation to total skull length

M. superciliosum	Skull length	Skull width(quadrates)	
B.M.(N.H.)			
R2030	634	185	3.42: 1
R2041	522	156	3.34: 1
R2055	480	135	3.55: 1
H.M.(U.G.)			
v964	560	173	3.23: 1
v985	599	197	3.04: 1
v1140	619	197	3.14: 1
C.M.P.			
R20	530 e	189	2.80: 1
M. moreli			
B.M.(N.H.)			
R2054	607	185	3.28: 1
H.M.(U.G.)			
v971	589	186	3.16: 1
v1143	595	177	3.36: 1
M. cultridens			
B.M.(N.H.)			
R3804	738	254	2.90: 1
M. brachyrhynchus			
C.M.P.			
R176	802	283	2.83: 1

M. sp.			
H.M.(U.G.)			
v966	550e	166	3.31: 1
v978	494e	167	2.95: 1
v987	632	204	3.09: 1
v1142	576	166	3.46: 1
v1004	680e	206	3.30: 1

CHARACTER 2

Width between the outer angles of the prefrontals in relation to total skull length

M. superciliosum	Skull length	Skull width(prefrontals)	
B.M.(N.H.)			
R2030	634	150	4.22: 1
R2051	510	117	4.15: 1
R2041	522	114	4.57: 1
R2055	480	114	4.21: 1
C.M.P.			
R20	530e	128e	4.14: 1
H.M.(U.G.)			
v964	560	134	4.17: 1
v985	599	145	4.13: 1
v1015	590e	132	4.46: 1
v1140	619	139	4.45: 1
S.M.			
A	596	139	4.28: 1
M. moreli			
B.M.(N.H.)			
R2054	607	148	4.10: 1
R2044	575	130	4.42: 1

M. moreli (contd.)			
H.M.(U.G.)			
v971	589	148	3.97: 1
v1143	595	134	4.44: 1
M. laeve			
B.M.(N.H.)			
R3015	480	114	4.21: 1
R3014	450	90	5.00: 1
R2042	510	129	3.95: 1
M. cultridens			
B.M.(N.H.)			
R3804	738	255	2.89: 1
M. brachyrhynchus			
B.M.(N.H.)			
R3700	615	213	2.88: 1
R3699	635	224	2.83: 1
C.M.P.			
R176	802	208	3.85: 1
M. durobrivense			
B.M.(N.H.)			
R2618	425	149	2.85: 1
M. sp.			
H.M.(U.G.)			
v965	575 e	132	4.35: 1
v966	550 e	136	4.04: 1
v987	632	156	4.02: 1
v1142	576	129	4.46: 1
v1004	680 e	156	4.35: 1

CHARACTER 3

Distance between the premaxillae and nasals as a % of total skull length

M. superciliosum	Skull length	Distance:premax./nasals	%
B.M.(N.H.)			
R2030	634	90	14.19
R2051	510	55	10.78
R2041	522	55	10.53
R2055	480	70	14.58
H.M.(U.G.)			
v985	599	77	12.85
v1015	590	73	12.37
v1140	619	84	13.57
S.M.			
A	596	84	14.09
M. moreli			
B.M.(N.H.)			
R2054	607	74	12.19
R2032	595	79	13.27
R2044	575	60	10.43
H.M.(U.G.)			
v971	589	81	13.75
v1143	595	132	22.18
M. laeve			
B.M.(N.H.)			
R3015	480	100	20.83
R3014	450	95	21.11
R2042	510	80	15.68
M. cultridens			
B.M.(N.H.)			
R3804	738	58	7.85

M. brachyrhynchus			%
B.M.(N.H.)			
R3700	615	0	0.00
R3699	635	16	2.52
C.M.P.			
R176	802	33	4.11

M. durobrivense			
B.M.(N.H.)			
R2618	425	26	6.11

M. sp.			
H.M.(U.G.)			
v965	575	98	17.04
v966	550	62	11.27
v978	494	78	15.78
v987	632	50	12.64
v998	563	89	15.80
v1142	576	65	11.28

CHARACTER 4

Length of the nasals as a % of total skull length

M. superciliosum	Skull length	Length of nasals	%
B.M.(N.H.)			
R2030	634	213	33.50
R2051	510	200	39.21
R2041	522	195	37.35
R2055	480	170	35.41
H.M.(U.G.)			
v964	560	205 e	36.60
v985	599	232	38.73
v1015	590 e	255	43.22
v1140	619	222	35.86

			%
M. superciliosum (contd.)			
C.M.P.			
R20	530 e	218	41.13
S.M.			
A	596	174	29.19
M. moreli			
B.M.(N.H.)			
R2054	607	243	40.03
R2032	595	206	34.62
R2044	575	225	39.13
H.M.(U.G.)			
v971	589	253	42.95
v1143	595	184	30.92
M. laeve			
B.M.(N.H.)			
R3015	480	150	31.25
R3014	450	135	30.00
R2042	510	185	36.27
M. cultridens			
B.M.(N.H.)			
R3804	738	252	34.14
M. brachyrhynchus			
B.M.(N.H.)			
R3700	615	250	40.60
R3699	635	247	38.89
C.M.P.			
R176	802	339 e	42.26

M. durobrivense			%
B.M.(N.H.)			
R2618	425	148	34.82
M. sp.			
H.M.(U.G.)			
v965	575 e	213	37.04
v966	550 e	169	30.72
v987	632	256	40.50
v998	563	206	36.58
v1142	576	214	37.15

CHARACTER 5

Length of the mandibular symphysis as a % of the total length of the mandible

M. superciliosum	Mandible length	Length of symphysis	%
B.M.(N.H.)			
R2030	720	305	42.36
R3016	880	380	43.18
M. moreli			
B.M.(N.H.)			
R2054	720	360	50.00
R2032	670	270	40.29
R2044	635	270	42.51
H.M.(U.G.)			
v1143	636	294	46.22
M. cultridens			
B.M.(N.H.)			
R3804	809	340	42.02
M. sp.			
H.M.(U.G.)			
v1141	594	314	52.86

CHARACTER 6

Distance between the nasals and premaxillae as a % of the length of the nasals

M. laeve	Length of nasals	Distance:premax./nasals	%
B.M.(N.H.)			
R3015	150	100	66.66
R3014	135	95	70.37
R2031	163	90	55.21
M. leedsi			
B.M.(N.H.)			
R3899	194	100	51.54
R3540	200	85	42.50
M. moreli			
B.M.(N.H.)			
R2054	243	74	30.45
R2044	225	60	26.66
R2032	206	79	38.34
H.M.(U.G.)			
v971	253	81	32.01
M. superciliosum			
B.M.(N.H.)			
R2053	180	45	25.00
R2030	213	90	42.75
R2051	200	55	27.50
R2041	195	55	28.20
R2065	170	70	41.17
H.M.(U.G.)			
v985	232	77	33.18
v989	189	93	49.20

			%
M. superciliosum (contd.)			
H.M.(U.G.) (contd.)			
v1015	255	73	28.62
v1140	222	84	37.83
C.M.P.			
R10	247	71	28.74
R17	229	84	36.68
R42	198	79	39.89
R18	233	79	33.90
S.M.			
A	174	84	48.20
B	154	34	22.00
C	216	119	55.09
M. cultridens			
B.M.(N.H.)			
R3804	252	58	23.01
R3541	195	38	19.48
M. brachrhynchus			
B.M.(N.H.)			
R3700	250	0	0.00
R3699	247	16	6.47
C.M.P.			
R176	339	33	9.73
M. durobrivense			
B.M.(N.H.)			
R3321	196	18	9.18
R2039	187	25	13.36
R2618	148	26	17.56

M. sp.			%
H.M.(U.G.)			
v962	216	106	49.07
v965	213	98	46.00
v966	169	62	36.68
v978	206	78	37.86
v987	256	50	19.53
v998	206	89 e	43.20
v1000	242	89	36.77
v1142	214	65	30.37

Abbreviations

e	estimated value
B.M.(N.H.)	British Museum (Natural History)
H.M.(U.G.)	Hunterian Museum, University of Glasgow
C.M.P.	City Museum, Peterborough
S.M.	Sedgewick Museum, Cambridge

APPENDIX 2

INDEX OF MATERIAL EXAMINED

The specimens examined during the course of the study are listed below. The abbreviations used for the collections examined are as follows:

B.M.(N.H.)	British Museum (Natural History)
H.M.(U.G.)	Hunterian Museum, University of Glasgow
O.U.M.	Oxford University Museum
S.M.	Sedgewick Museum, University of Cambridge
D.C.M.	Dorset County Museum
W.H.	Wollaton Hall, Nottingham
N.M.W.	National Museum of Wales, Cardiff
C.M.P.	City Museum, Peterborough
M.B.	Private Collection of M. Bishop, Kilmarnock
M.O.	Private Collection of M. Oates, London

* denotes type specimen

** all page numbers refer to Andrews (1913)

SPECIES	R. NO.	MATERIAL EXAMINED	GEOGRAPHIC AND STRATIGRAPHIC LOCALITY
B.M.(N.H.)			
S. leedsi *	R3320	see p.119 **	Oxford Clay, Peterboro'
S. leedsi	R3806	see p. 119**	" " "
S. leedsi	R2619	see p.121 **	" " "
S. hulkei *	R2074	see p.123 **	" " "
S. durobrivensis *	R3701	see p.126 **	" " "
S. durobrivensis	R2865	see p.128 **	" " "
S. durobrivensis	R2705	see p.129 **	" " "
S. durobrivensis	R2076	see p.129 **	" " "
S. durobrivensis	R2073	see p.130 **	" " "
S. obtusidens *	R3168	see p.133 **	" " "
S. obtusidens	R3169	see p.134 **	" " "
S. obtusidens	R3898	see p.135 **	" " "
M. nasutus *	R2617	see p.141 **	" " "
M. nasutus	R3892	see p.142 **	" " "
M.B.			
M. nasutus	M.B.1	most of the post axial vertebrae; pelvic girdle & hind limbs	" " "
B.M.(N.H.)			
M. laeve *	R3015	see pp.192/3 **	" " "
M. laeve	R3014	see p.193 **	" " "
M. laeve	R2042	see p.195 **	" " "
M. laeve	R2031	see p.195 **	" " "
M. leedsi *	R3540	see p.196 **	" " "
M. leedsi	R3899	see p.196 **	" " "

M. cultridens *	R3540	see p.197 **	Oxford Clay,	Peterboro'	
M. cultridens	R3541	see p.198 **	"	"	"
M. brachyrhynchus ***			"	"	"
M. brachyrhynchus	R3700	see p.199 **	"	"	"
M. brachyrhynchus	R3699	see p.199 **	"	"	"
M. brachyrhynchus	R3939	see p.199 **	"	"	"
M. durobrivense *	R1994	see p.200 **	"	"	"
M. durobrivense	R3321	see p.200 **	"	"	"
M. durobrivense	R2039	see p.200 **	"	"	"
M. durobrivense	R2618	see p.201 **	"	"	"
M. moreli ****					
M. moreli	R2054	see p.188 **	"	"	"
M. moreli	R2032	see p.190 **	"	"	"
M. moreli	R2044	see p.190 **	"	"	"
M. moreli	R2049	see p.191 **	"	"	"
M. moreli	R3900	see p.191 **	"	"	"
M. moreli	R1666	see p.191 **	"	"	"
M. moreli	R2040	see p.192 **	"	"	"
M. superciliosum *****					
M. superciliosum	R2030	see p.181 **	"	"	"
M. superciliosum	R2051	see p.181 **	"	"	"
M. superciliosum	R1530	see p.183 **	"	"	"
M. superciliosum	R2033	see p.184 **	"	"	"
M. superciliosum	R3016	see p.185 **	"	"	"
M. superciliosum	R2053	see p.186 **	"	"	"

*** for type specimen see E. E. Deslongchamps (1867) p.333, pl.xxiii figs. a - d

**** for type specimen see E. E. Deslongchamps (1867) p.320, pl.xxi figs. 4 & 5, pl.xxii figs. 1 & 2

*****

M. superciliosum (contd.)					
M. superciliosum	R2041	see p.186 **	Oxford	Clay,	Peterboro'
M. superciliosum	R2055	see p.186 **	"	"	"
M. superciliosum	R1529	see p.186 **	"	"	"
M. superciliosum	R2065	see p.187 **	"	"	"
M. superciliosum	R2048	see p.187 **	"	"	"
M. superciliosum	R2069	see p.187 **	"	"	"
M. superciliosum	R2056	see p.187 **	"	"	"
M. superciliosum	R2036	see p.187 **	"	"	"
M. superciliosum	R2058	see p.187 **	"	"	"
M. superciliosum	R2064	see p.187 **	"	"	"
M. superciliosum	R2080	see p.187 **	"	"	"
M. superciliosum	R2775	see p.187 **	"	"	"
M. superciliosum	R2062	see p.188 **	"	"	"
M. superciliosum	R2077	see p.188 **	"	"	"
H.M.(U.G.)					
Steneosaurus sp.	v840	scutes & post cranial fragments	"	"	"
Steneosaurus sp.	v841	cervical & dorsal ribs	"	"	"
Steneosaurus sp.	v842	fragmentary head	"	"	"
	v840, 841 and 842 possibly belong together				
M. superciliosum	v930	mandible & rostrum	Oxford	Clay,	Peterboro'
			Dogsthorpe Pit		
M. superciliosum	v931	centrum	Oxford	Clay,	Peterboro'
Metriorhynchus sp.	v932	fragmented mandible	"	"	"
M. sp.	v933	centrum	"	"	"
M. sp.	v934	centrum	"	"	"
M. sp.	v934	centrum	"	"	"

M. sp.	v935	centrum	Oxford Clay, Peterboro'
M. sp.	v936	centrum	" " "
M. sp.	v937	centrum	" " "
M. sp.	v938	femora	" " "
M. sp.	v939	ischium	" " "
M. sp.	v940	ischium	" " "
M. sp.	v941	pelvic girdle & hind limb	Oxford Clay, Peterboro' 1891 Pit 5
M. sp.	v942	fragmentary skull	Oxford Clay, Peterboro'
M. sp.	v943	left femur	" " "
M. sp.	v944	left femur	" " "
M. sp.	v945	femora	" " "
M. sp. (juvenile?)	v946	left femur	" " "
M. sp.	v947	ilium	" " "
M. sp.	v948	fragmentary skull and jaws	" " "
M. sp.	v949	centrum	" " "
M. sp.	v950	ischia	" " "
M. sp.	v951	jaw fragments	" " "
M. sp.	v952	ilium	" " "
M. sp.	v954	mandible	" " "
M. sp.	v956	quadrate	" " "
M. sp.	v957	right femur	" " "
M. sp.	v958/9	fragmentary bones	" " "
M. sp.	v960	scapula, femora & pelvic girdle	" " "
M. sp.	v962	fragmentary head & jaws	" " "
M. superciliosum	v963	skull & jaws centra & ilium	" " "

M. superciliosum	v964	imperfect skull & centra	Oxford Clay, Peterboro' 1906 Pit 19
M. superciliosum	v965	skull & mandible	Oxford Clay, Peterboro'
M. sp.	v966	skull & mandible	" " "
M. sp.	v967	imperfect mandible	" " "
M. sp.	v968	imperfect mandible	" " "
M. sp.	v969	imperfect mandible	" " "
M. sp.	v970	imperfect mandible	" " "
M. moreli	v971	well preserved skull	" " "
M. sp.	v972	imperfect mandible, ribs, vertebrae & pelvic girdle	Dogsthorpe Pit 1906 Oxford Clay, Peterboro' Pit 1
M. sp.	v973	skull & mandible	Oxford Clay, Peterboro'
M. sp.	v974	skull fragments	" " "
M. sp.	v975	skull fragments	" " "
M. sp.	v978	skull & mandible	" " "
M. sp.	v979	fragmentary skull	" " "
M. sp.	v981	fragmentary skull	" " "
M. sp.	v982	skull & mandible	" " "
M. sp.	v984	skull & fragmentary mandible	" " "
M. sp.	v983	fragmentary skull	" " "
M. superciliosum	v985	well preserved skull & mandible	" " "
M. sp.	v986	left femur	" " "
M. sp.	v987	fragmentary skull & mandible	" " "
M. sp.	v988	fragmentary skull & mandible	" " "

M. superciliosum	v989	fragmentary skull & mandible	Oxford Clay, Peterboro'
M. sp.	v990	skull, pectoral & pelvic girdle & hind limb & caudal vertebrae	" " " Eastwood Pit ? 1913
M. superciliosum	v993	imperfect skull & mandible, incomplete pelvic girdle, ribs femora & vertebrae	Oxford Clay, Peterboro'
M. sp.	v995	fragmentary skull & mandible, pelvic girdle, hind limbs & vertebrae	" " "
M. sp.	v961	left femur	" " "
M.sp.	v996	fragmentary skull	" " "
M. sp.	v997	assorted vertebrae	" " "
M. sp.	v998	fragmented skull, pelvic girdle, hind & forelimbs & vertebrae	" " " Pit 17, 1903
M. sp.	v1000	skull & mandible imperfect ribs	Oxford Clay, Peterboro' Pit 13, 1909
M. sp.	v1001	ribs, vertebrae & femora	Oxford Clay, Peterboro'
M. sp.	v1002	fragmentary mandible	" " "
M. sp.	v1003	rib & vertebrae fragments	" " "
M. sp.	v1004	well preserved skull & mandible	" " "

M. sp.	v1005	fragmentary mandible, vertebrae, pectoral & pelvic girdles, femora	Oxford Clay,	Peterboro'	Pit 8 1890
M. sp.	v1006	pelvic girdle, ribs, vertebrae, right femur	Oxford Clay,	Peterboro'	
M. sp.	v1009	fragmentary skull & mandible	"	"	"
M. sp.	v1010	fragmentary skull & mandible	"	"	"
M. sp.	v1011	fragmentary skull & mandible	"	"	"
M. sp. (juvenile?)	v1012	fragmentary skull & mandible	"	"	"
M. sp.	v1013	pectoral & pelvic girdles, femora, ribs, vertebrae & teeth	"	"	"
M. superciliosum	v1015	fragmentary skull & mandible, pectoral girdle, ischium & femora	"	"	"
M. sp.	v1016 - v1028	fragmentary remains	"	"	"
M. sp.	v1023	remains of a very small & presumably young crocodile	"	"	"
M. superciliosum	v1140	almost complete, partly restored, anterior part of jaw bitten off, pectoral girdle, forelimbs, hind limbs, ribs and vertebrae	"	"	"

M. sp.	v1142	well preserved skull & mandible, pelvic girdle, left femur & vertebrae	Oxford Clay,	Peterboro'	
M. moreli	v1143	well preserved skull & mandible, pectoral girdle, humerus & vertebrae	"	"	"
M. sp.	v1144	teeth	"	"	"
M. sp.	v1145	humerus, ilium, femur, teeth	"	"	"
M. sp.	v1146	pectoral girdle, ilium & humerus	"	"	"
Steneosaurus sp.	v1151	pelvic girdle	"	"	"
S. sp.	v1152	scutes	"	"	"
S. sp.	v1153	slender, pointed teeth	"	"	"
S. sp.	v1401	selection of teeth of varying degrees of bluntness	"	"	"
S. sp.	v1405	slender, recurved teeth	"	"	"
S. sp.	v1429	large, blunt teeth	"	"	"
Metriorhynchus sp.	v1430 - v1437	selection of teeth	"	"	"
M. sp.	v1141	imperfect mandible & teeth	"	"	"
Steneosaurus sp.	v1606	rib fragments	"	"	"
S. leedsi	v1150	extremely well preserved skull	"	"	"

O.U.M.			
S. boutilieri	J1401	complete rostrum & orbital region	Upper Great Oolite Gibralter Quarry near Oxford
S. boutilieri	J1403	well preserved skull	Great Oolite, Enslow Bridge, Oxford
S. boutilieri	J1416	mandible	Great Oolite, Enslow Bridge, Oxford
S. meretrix *	J29850	well preserved skull & mandible	Great Oolite, Enslow Bridge, Oxford
S. meretrix	J29851	well preserved skull	Great Oolite, Enslow Bridge, Oxford
S. meretrix	J1407	symphysial portion of the mandible	Great Oolite, Enslow Bridge, Oxford
S. depressus *	J1420	well preserved skull & mandible, vertebrae ribs, imperfect pelvis & left hind limb	Oxford Clay, Jason zone, Peterboro'
S. megistorhynchus	J1414	mandible only	Lower Great Oolite, Enslow Bridge, Oxford
Steneosaurus sp.	M.O.1	imperfect rostrum	Kirklington Quarry, near Oxford
S.M.			
M. superciliosum	A	imperfect skull	Oxford Clay, Whittlesea
M. superciliosum	B	imperfect skull	Oxford Clay, Fletton
M. sp.	C	imperfect skull	No data
M. hastifer	J18212	anterior end of rostrum	Kimmeridge Clay, Chettisham, Ely

M. superciliosum	J64398	imperfect skull	Oxford Clay,	Peterboro'
Mycterosuchus nasutus	1	skull, imperfect pelvis, humerus scutes & vertebrae	"	" "
Steneosaurus sp.	J63870	fragmentary skull & mandible	"	" Whittlesea
S. sp.	J63869	fragmentary skull & mandible	"	" "
S. sp.	J63873	fragmentary skull & mandible	"	" "
S. sp.	J63871	fragmentary skull & mandible	"	" "
S. sp.	J63875 - J63879	dorsal vertebrae	"	" "
Metriorhynchus sp.	J64266	fragmentary skull, showing intermediate ornament of dorsal bones	"	" "
D.C.M.				
S. purbeckensis *	-	imperfect skull, anterior part of rostrum missing	Middle Purbeck, Swanage area (Woodward & Sherborne)	
S. sp.	G113 G113/1	imperfect skull part of rostrum, parietal and squamosal bones	Oxford Clay, Browns Brickfield, Putton Lane, Chickerell Dorset	
	G113/2 - G113/58	30 imperfect vertebrae, ribs scutes & imperfect left ilium		

Steneosaurus sp.	-	fragmentary remains	Kimmeridge Clay, Kimmeridge Bay, 10ft. from basal cliff exposure
S. sp.	G122A	crushed skull, large striated, pointed slightly recurved teeth	Kimmeridge Clay, Dorset
	G122B	large portion of right mandible of specimen above	
S. sp.	G116	imperfect mandible	Kimmeridge Clay, Ringstead Bay, Dorset
S. sp.	G96/1	rostrum & fragmentary post cranial elements	
S. sp.	G114A	fragmentary skull	Kimmeridge Clay,
	G114	fragmentary mandible	Ringstead Bay, Dorset
W.H.			
Steneosaurus sp.	659	imperfect tibia	Oxford Clay, Peterboro'
S. sp.	663	cervical & dorsal vertebrae	" " "
S. durobrivensis	664	imperfect skull	" " "
S. sp.	665	imperfect mandible	" " "
S. sp.	666	articular & angular	" " "
S. sp.	667	exoccipital & basiocciptal bones	" " " Fletton
S. sp.	668	associated limb bones & series of scutes	Oxford Clay, Peterboro'

Metriorhynchus sp.	671	fragmentary mandible	Oxford Clay, Peterboro'
M. sp.	672	vertebrae	" " "
M. moreli	673	fragmentary skull	" " "
M. sp.	675	imperfect mandible	" " "
M. sp.	676	fragmentary skull	" " Whittlesea
M. sp.	677	fragmentary skull	" " Peterboro'
M. sp.	678	fragmentary skull	" " "
M. sp.	679	fragmentary skull	" " "
M. sp.	680	fragmentary skull	" " "
N.M.W.			
M. superciliosum	19.96.G4	imperfect skull & associated limb bones	" " "
M. moreli	-	imperfect skull	no data
M. leedsi	21.44.G4	imperfect skull & right humerus, coracoid, femora, ischia, pubes, 5 cervical, 13 dorsal, 9 caudal vertebrae	Oxford Clay, Whittlesea Cambs.
M. sp.	19.96.G15	femora, imperfect pelvis, humeri, scapulae & series of vertebrae & ribs	Oxford Clay, Peterboro'
M. sp.	19.96.G15x	left femur, series of vertebrae & ribs	" " "
M. sp.	19.96.G15a	femora, right ilium & pubis, imperfect right coracoid, scapula, vertebrae, ribs & chevrons	" " " Hicks & Gardener Pit

Steneosaurus sp.	19.96.G12a	imperfect skull with teeth showing form of crown in relation to size of skull	Oxford Clay, Peterboro'
C.M.P.			
S. leedsi	R75	skull, atlas,axis, 11 vertebrae, scutes	" " " Fletton, Phillips Collection
S. leedsi	R136	imperfect skull & mandible	Oxford Clay, Peterboro' Fletton
S. leedsi	R179	imperfect skull & toothed mandible	Oxford Clay, Peterboro' Kings Dyke
S. durobrivensis	R175	almost complete skeleton	Oxford Clay, Yaxley Phillips Collection
S. obtusidens	R178	almost complete skeleton	Oxford Clay, Peterboro' presented to L.B.C.1923
S. sp.	R1	imperfect skeleton.	Oxford Clay, Eye Phillips Collection
S. sp.	R39	imperfect skull & 4 vertebrae	Oxford Clay, Peterboro' Phillips Collection
S. sp.	R64	12 associated vertebrae & 11 scutes	Oxford Clay, Peterboro' Fletton, Phillips Collection
S. sp.	R123	crushed vertebrae	Oxford Clay, locality unknown
S. sp.	R127	crushed vertebrae	Oxford Clay, locality unknown
M. brachyrhynchus	R176	imperfect skull & teeth	Oxford Clay, locality unknown, Phillips Collection

M. superciliosum	R17	broken skull & mandible, vertebrae & limb bones	Oxford Clay, locality unknown, Phillips Collection
M. superciliosum	R42	large broken skull	Oxford Clay, locality unknown, Phillips Collection
M. superciliosum	R180	small median region of skull	Oxford Clay, locality unknown, Phillips Collection
M. superciliosum	R18	broken skull & toothed mandible	Oxford Clay, Peterboro' Kings Dyke, Phillips Collection
M. superciliosum	R20	imperfect skull & mandible	Oxford Clay, Peterboro' Phillips Collection
M. sp.	R32	broken skull & mandible, 17 vertebrae	Oxford Clay, Peterboro' Fletton, Phillips Collection
M. sp.	R135	imperfect skull	Oxford Clay, Peterboro' Yaxley, Phillips Collection
M. sp.	R181	imperfect mandible	Oxford Clay, Peterboro' Phillips Collection
M. sp.	R63	limb bones & sclerotic plates	Oxford Clay, Peterboro' Kings Dyke, Phillips Collection

M. brachyrhynchus	R38	42 vertebrae	Oxford Clay, locality unknown
M. brachyrhynchus	R60	imperfect mandible	Oxford Clay, Peterboro' Kings Dyke, Phillips Collection
M. brachyrhynchus	R76	vertebrae, limb bones imperfect pectoral girdle	Oxford Clay, Peterboro' Kings Dyke, Phillips Collection
M. durobrivense	R19	posterior half of imperfect skull	Oxford Clay, Peterboro' Kings Dyke, Phillips Collection
M. leedsi	R24	imperfect skull	Oxford Clay, Peterboro' Kings Dyke, Phillips Collection
M. leedsi	R72	large broken skull	Oxford Clay, Peterboro' Kings Dyke, Phillips Collection
M. superciliosum	R6	fragmentary skull & teeth	Oxford Clay, Peterboro' Farcet, Phillips Collection
M. superciliosum	R74	broken skull & toothed mandible	Oxford Clay, Peterboro' Phillips Collection
M. superciliosum	R8	broken skull & toothed mandible	Oxford Clay, Peterboro' Fletton, Phillips Collection
M. superciliosum	R10	broken skull & toothed mandible	Oxford Clay, Peterboro' Fletton, Phillips Collection
M. superciliosum	R7	fragmentary skull	Oxford Clay, locality unknown

APPENDIX 3

POST CRANIAL DATA FOR STENEOSAURUS AND METRIORHYNCHUS

TABLE 34

Specimen	Head	Axis + atlas	No. of post axial vertebrae	Cervical total length	No. of dorsal vert.	Dorsal total length
R3806	853		7	353	12	769*
R3701	740	86	7	321	14	714
R178						
C.M.P.	1030	102	7	439	10	1022*
R175						
C.M.P.	1112	100	4	441*	17	1072
R3892					15	951
1 M.B.			4	180*	10	639*
R2054	607	63	5	188	17	712*
R2051	510		4	132*	17	561
R1530			5	172	16	613
R6859		60	5	166	17	685
v998						
H.M.(U.G.)		48	4	153	17	550
v1142	576	56	5	169	16	582
v1006		69	5	205	16	723
v1143			4	153	16	708
v1013		61	4	151	17	590
v960		51	5	197	16	662
v1140			5	182	14	657*

* estimated values based on 7 cervical vertebrae (Stenecosaurus)

5 cervical vertebrae (Metriorhynchus) and 17 dorsal vertebrae

TABLE 34 (contd.)

Specimen	No. of sacral vertebrae	Sacral total length	No. of caudal vertebrae	Caudal total length(preserved)
R3806	2	93	36	1535
R3701	2	93	38	1521
R178				
C.M.P.	2	119	38	1746
R175				
C.M.P.	2	119	36	1690
R3892	2	117	35	1594
1 M.B.	2	110*	36	1578
R2054	2	86	28	933
R2051	2	64	30	802
R1530	2	74	35	1094
R6859			29	982
v998				
H.M.(U.G.)			12	421*
v1142	2	64*		
v1006	2	80*		
v1143				
v1013	2	58		
v960	2	74		
v1140				

* estimated values

BODY PROPORTIONS - Supplement to Table 34

Comparisons between Metriorhynchus, Steneosaurus, Alligator, Gharial and Protosuchus are presented below, by taking cervical/dorsal/caudal lengths of each animal as 100, and scaling head, tail and limb proportions as follows: (after M^{c}Leod pers. comm. 1975)

	Protosuchus*	Metriorhynchus	Steneosaurus	Alligator*	Gharial
head	38	57.0	63.4	45	41
trunk	100	100	100	100	100
tail	134	110.2**	120.5**	131	110
forelimb	57	16.6	36.4	52	31
hindlimb	89	52.2	57.6	65	46

* unpublished data (M^{c}Leod 1975)

** maximum number of caudal vertebrae known, although not a complete series

All figures for Metriorhynchus and Steneosaurus are averages, based on the measurements presented in full in appendix 3.

Detailed quantitative data on body proportions, proportions within limbs and numbers of vertebrae are also contained in appendix 3 (in addition to raw data on post cranial measurements).

The exact number of vertebrae for either genera is not known, owing to the nature of preservation of Callovian material (and methods of recovery and excavation). Andrews (1913) states that the maximum number of dorsal vertebrae found together was 17 and suggests that there were, in addition, one or two lumbars. In recent crocodiles, the first dorsal vertebra is defined as that one whose ventral rib is joined to the sternum. Since this is a cartilagenous join, it is not preserved in the fossil material and Andrews (1913) defines the dorsal vertebrae as those in which the parapophysis is borne on the transverse process, and as cervical, those in which it is borne on the centrum.

In the course of this research, specimens with the following maximum numbers of vertebrae were examined:

	Steneosaurus	Metriorhynchus
cervical (post axial)	7	5
dorsal	15 (+2 lumbars)*	15 (+2 lumbars)*
sacral	2	2
caudal	38	35 **

* vertebrae showing no facets for rib attachment

** Fraas (1902) documents 44 for Geosaurus

The information contained in the table above can be compared with data on Alligator and Protosuchus (M^{c}Leod 1975 unpubl. data.):

	Protosuchus	Alligator
cervical	10	9
dorsal	14	16
sacral	2	2
caudal	39 *	35 **

* maximum number known

** average number

DEFINITION OF THE POST CRANIAL MEASUREMENTS

Scapula width

The width of the distal edge, from the most anterior to the most posterior point of the distal surface.

Scapula length

The maximum proximo-distal length, measured parallel to the long axis of the bone.

Humerus length

Maximum proximo-distal length measured parallel to the long axis of the shaft from the most proximal point of the proximal surface to the most distal point on the distal surface.

Length to the delto-pectoral crest

The maximum proximo-distal length measured point to point between the head of the humerus and the most distal point of the crest.

Minimum width of the humerus

The minimum antero-posterior distance of the shaft, measured at right angles to the long axis of the shaft.

Ulna length

The maximum proximo-distal length measured parallel to the long axis of the bone in the steneosaurs, but point to point in the metriorhynchids because the bone has become sub-circular in shape.

Ulna width

For the steneosaurs this corresponds to the minimum width of the humerus, in the metriorhynchids it is measured point to point from the pre-axial side to the post-axial side of the bone.

Radius length

The maximum proximo-distal length measured parallel to the long axis of the shaft in Steneosaurus, while in Metriorhynchus it is measured point to point from the proximal to the distal border of the bone.

Length of the dorsal border of the ilium

The maximum antero-posterior length of the border from the most anterior point of the anterior process of the ilium to the most posterior point on the border.

Width of the ischium

The maximum width of the distal border of the ischium measured point to point from the most anterior to the most posterior point on the distal border.

Ischium length

The maximum dorso-ventral length of the posterior edge of the ischium measured point to point from the most proximal point of the proximal articular surface to the most distal point of the distal border.

Pubis length

The maximum proximo-distal length of the pubis, measured at right angles to the long axis of the shaft.

Pubis width

Measured point to point from the most anterior to the most posterior point of the distal expansion.

Femur length

The maximum length measured parallel to the long axis of the shaft, between the head and distal condyles.

Width of head of femur

Measured point to point between the most anterior and posterior surfaces of the head.

Width of femur

The minimum width of the shaft, measured antero-posteriorly at right angles to the long axis of the shaft.

Tibia length

Maximum proximo-distal length measured parallel to the long axis of the shaft.

Minimum width of the tibia

Measured at right angles to the long axis of the shaft.

Fibula length

(see tibia length)

Calcaneum and astragulus length

The maximum length measured point to point between the most proximal point on the proximal surface and most distal point on the distal surface.

Lengths of metatarsals, metacarpals and phalanges

The maximum proximo-distal length parallel in each case to the long axis of the bone shaft.

Dimensions of the vertebrae

Length

Taken in mid ventral line, measured parallel to the long axis of the centrum from the most anterior point on the ventral surface to the most posterior point on the ventral surface.

Width

The maximum width of the anterior face of the centrum.

Height

The maximum dorso-ventral length measured parallel to the long axis of the neural spine, between the most proximal point on the proximal surface of the neural spine to the most distal point on the distal surface of the centrum.

Width of the transverse processes

The maximum width between the outer edges of the transverse processes, measured parallel to the long axis of the transverse processes.

TABLE 35

Specimen	Humerus	Radius	Ulna	Ulnare	M.C.	Phalanges	Total length
R3806	128	67	88				
R3701	122	71	89				
R175							
C.M.P.	186	101	99				
R178							
C.M.P.	197	94	125				
S.M.1	188	102	116				
R2617	211	113	142				
1 M.B.	189*	106*					
R3014	43						
R2051	57						
R1530	87						
R3016	67	22		19	26	27?	161**
v998	59*						
v1005	72						
v1143	64						
v1146	81						
v1140	70	24	27*	14	28	48	211***

Total length = humerus length + radius length + ulnare length + metacarpal (M.C.) length + phalange length.

* estimated value

** 2.39 x humerus length

*** 3.01 x humerus length

TABLE 36

Specimen	Femur	Tibia	Fibula	Astrgls.	Calcn.	M.T.	Phlngs.*	T.L.
R3806	303	153	141		28	115	88	687
R3701	314	140	129	29	24	103	97	678
R175								
C.M.P.	416	187	167	33	30	141		
R178								
C.M.P.	421	204	169		32*	144	130	931
S.M.1	391	181	171	30	132			
R2617	400	198	178		36	141		
1 M.B.	379	167	159	33	24	129	92	791
v1151								
H.M.(U.G.)	352	156*	140*					
v840								
H.M.(U.G.)	392	172						
R3014	174	66	65	14	12	63	80	395
R2618	169	73			14	68	84	408
R2054	261	89	85		21	88	109	653
R2051	191	66*	63		34*	67	74	495
R1530	266	93	89		21	93	104	666
R6859	229	79				96		
v990								
H.M.(U.G.)	182	61	59			61		
v1013								
H.M.(U.G.)	258	87						

TABLE 36 (contd.)

T.L. = Femur length + tibia length + calcaneum length + metatarsal (M.T.) length + phalange (phlngs.) length (* estimated)

* estimated value

Astrgls. astragulus Calcn. calcaneum

Relationship between femur length and total length of hind limb

STENEOSAURUS

R3806	hind limb = 2.3 x femur length
R3701	hind limb = 2.2 x femur length
R178	
C.M.P.	hind limb = 2.2 x femur length
1 M.B.	hind limb = 2.1 x femur length

METRIORHYNCHUS

R3014	hind limb = 2.3 x femur length
R2618	hind limb = 2.4 x femur length
R2054	hind limb = 2.5 x femur length
R2051	hind limb = 2.6 x femur length
R1530	hind limb = 2.5 x femur length

TABLE 37

The relationship between the length between the proximal end of the humerus and the delto-pectoral crest, and the total length of the humerus.

STENEOSAURUS

humerus length ÷ length to delto-pectoral crest

R3806 = 3.02

R3701 = 3.12

R178 C.M.P. = 3.22

R175 C.M.P. = 3.04

R2617 = 3.45

METRIORHYNCHUS

humerus length ÷ length to delto-pectoral crest

R2051 = 2.14

R1530 = 2.12

R2032 = 2.32

21.44.G4 N.M.W. = 1.94

G114 D.C.M. = 2.08

A S.M. = 2.25

v1005 H.M.(U.G.) = 2.18

v1143 H.M.(U.G.) = 1.88

v1146 H.M.(U.G.) = 2.18

v1140 H.M.(U.G.) = 2.41

N.B. R numbers refer to B.M.(N.H.) material unless otherwise indicated

TABLE 38

POST CRANIAL MEASUREMENTS

IN STENEOSAURUS

	B.M.(N.H.) R 3806	R2619	R2074	R3701	R2865	R2076	R3168	R3169	R3898
Scapula width:									
proximal end	22			28			49	55	
Scapula length	102			91			167	150	
Humerus length	130	103		122					
Length to delto									
pectoral crest	43			39					
Humerus width:									
proximal end	52	38		31					
Minimum humerus width	17			18					
Ulna length	89			89				119	
Ulna width:									
proximal end	37							55	
Length, dorsal									
border of ilium	94	77	78	95		108	161	122	190
Ischium length	121		99	128	162		244		
Ischium width:									
distal expansion	122		101	135*	164		240		
Pubis length	130	100	108	126	166			195	
Pubis width:									
distal expansion	67	47	40	62	79	73	97	72	
Femur length	302	250	248	314	385	355	456	417	530
Length to 4th trochanter	51		49	76	93	82		97	
Femur width:proximal end	53	42	42	50	74	63	79	64	95
Minimum femur width	21	17	17	23	34	28	35	40	40*
Tibia length	153	116	113	140	176	171	213	197	
Fibula length	143			129		159			
Minimum tibia width	22		17	23	25	26		33	

TABLE 38 (contd.)

POST CRANIAL MEASUREMENTS IN STENEOSAURUS	R2617 S.M. 1	C.M.P. R178	R175	O.U.M. J1420	1 M.B.	H.M.(U.G.) v840	v1151
Scapula width:							
proximal end	59		48				
Scapula length	135	156	147				
Humerus length	211	188 197	186		189*		
Length to delto							
pectoral crest	61	78 61	61				
Humerus width:							
proximal end	70	52 62	64		64		
Minimum humerus width	23	21 23	24				
Ulna length	143	116 125	99				
Ulna width:proximal end	49	29	48				
Length, dorsal							
border of ilium			124	91	104		
Ischium length		161	195	139			
Ischium width:							
distal expansion		163	205				
Pubis length		145* 206	206		156		
Pubis width:							
distal expansion		72 103	103		55		
Femur length	400	391 421	416	294	379	392	352
Length to 4th trochanter				66			
Femur width:proximal end	68	64 75	67	52	66	69	51
Minimum femur width	21	31 42	39	30	34	43	30
Tibia length	200	181 204	187		167	172	156
Fibula length	178	171 179	167		159		140
Minimum tibia width		23 31	29		24	26	23

TABLE 39

POST CRANIAL MEASUREMENTS IN METRIORHYNCHUS

	B.M.(N.H.)	R 2051	R 1530	R 3016	R 2054	R 3014	R 3804	R 2618	R 2032	R 6859
Scapula width:										
proximal end		13	19			8				
Scapula length		56	79	87		60				
Humerus length		58	83	98		43				79
Length to delto pectoral crest		27	39							34
Humerus width:										
proximal end		17	20	25		10				20
Minimum humerus width		13								
Ulna length				37						
Ulna width:proximal end				27						
Length, dorsal border to ilium		38	52	48		46	28	33		41
Ischium length		82	112	114						106
Ischium width:										
distal expansion		87*	118							100
Pubis length		78	98	110		130	77	111		
Pubis width:										
distal expansion		29	57	50		67	39	44*		
Femur length		193	264	260	178	310	170	250		229
Length to 4th trochanter		35	44	47	32	69	34	46		42
Femur width:proximal end		34	40	40	31	52	29	44		36
Minimum femur width		20	25	28	11	28	15	25		23
Tibia length			92	89	68		73			
Fibula length		63	90	87	68					
Minimum tibia width			19	13			10			

TABLE 39 (contd.)

POST CRANIAL MEASUREMENTS IN METRIORHYNCHUS	N.M.W. 21.44.G4	19.96.G15a	H.M.(U.G.)	v990	v993	v1013	v1146	v1145	v1005	v1006
Scapula width:										
proximal end		24								
Scapula length		79				84				
Humerus length	72	71				83	81	72		
Length to delto										
pectoral crest	37	32				37		33		
Humerus width:										
proximal end	19	24				34		23		
Minimum humerus width	17	15				28		16		
Ulna length										
Ulna width:proximal end										
Length, dorsal										
border to ilium			39	43	44	41	43	49	47	
Ischium length		96	88	95*				117		
Ischium width:										
distal expansion				90*	94			110		
Pubis length	103	94		98				106		
Pubis width:										
distal expansion	42			36				51	61	
Femur length	236	227	182	223	256		269	243	261	
Length to 4th trochanter	65				61		62			
Femur width:proximal end	40	34	33	35			44	43	47	
Minimum femur width	25	22	20	25			26	22	29	
Tibia length			61							
Fibula length			59							
Minimum tibia width			12							

TABLE 39 (contd.)

POST CRANIAL MEASUREMENTS

IN METRIORHYNCHUS

	v1143	v1013	v941	v960	v1140
Scapula width:					
proximal end				21	21*
Scapula length				74	66*
Humerus length	64				70
Length to delto					
pectoral crest	34				29
Humerus width:					
proximal end	19				21
Minimum humerus width	14				
Ulna length					27*
Ulna width:proximal end					
Length, dorsal					
border to ilium		45	51		
Ischium length		123	125		
Ischium width:					
distal expansion		97	129		
Pubis length			87		
Pubis width:					
distal expansion			41		
Femur length	271	258	261	224	232
Length to 4th trochanter					
Femur width:proximal end	46	43	32	34	
Minimum femur width	25	27	19	26	
Tibia length	87				
Fibula length					
Minimum tibia width	16				

APPENDIX 4

CLASSIFICATION OF SPORES, POLLEN AND DINOFLAGELLATES OBTAINED FROM THE LOWER OXFORD CLAY FROM THE EAST MIDLANDS OF ENGLAND

Anteturma : Proximegerminates

Turma : Triletes

Subturma : Azonotriletes

Infraturma : Laevigati

Spores classified in this Infraturma are characterised by a smooth, or almost smooth, exine.

Genera :

Todisporites Couper (1958) p. 134 pl. 16 fig. 6

Botanical affinities:

Group : Filicalean

Family : Osmundaceae (Couper 1958)

Deltoidospora Miner (1935) p. 618 pl. 24 fig. 7 (and pl. 39 figs. 11 & 12)

Botanical affinities:

Group : Filicalean

Family : Cyatheaceae/Dicksoniaceae (Harris 1961)

Triplanosporites Pflug in Thomson & Pflug (1952) p. 58 pl. 3 fig. 7 (and pl. 39 fig. 1)

Botanical affinities:

Group : Filicalean

Family : Cyatheaceae/Dicksoniaceae (Couper 1958)

Cibotiumspora Chang (1965) p. 164 illustration: Malyavakina (1949) p. 50 pl. 7 fig. 21

Botanical affinities:

Group : Filicalean

Family : Dicksoniaceae (Filatoff 1975)

Concavisporites Pflug in Thomson & Pflug (1953) p. 49 pl. 1 fig. 19

(and pl. 39 fig. 4)

Botanical affinities:

Group : Filicalean

Family : possibly Cyatheaceae/Dicksoniaceae (Couper 1958)

Obtusisporis Krutzch (1959) emend. Pocock (1970) p. 135 illustration :

Potonie (1934 b) pl. 6 fig 1 (and pl. 39 figs. 6 and 7)

Botanical affinities:

Group : Filicalean

Family : Dicksoniaceae (Couper 1958)

Infraturma : Apiculati

These spores are sculptured with discrete elevations including granula, spina, bacula and capilli.

Genera :

Osmundacidites Couper (1958) p. 20 pl. 1 fig. 5

Botanical affinities:

Group : Filicalean

Family : Osmundaceae (Couper 1958, Harris 1961, Filatoff 1975)

Concavissimisporites Delcourt & Sprumont (1955) p. 25 pl. 2 fig. 1

(and pl. 39 fig. 13 and 40 figs. 1 - 3 and 8)

Botanical affinities:

Group : Filicalean

Family : Schizaeaceae (Couper 1958) / Dicksoniaceae (Erdtman 1957)

Infraturma : Murornati

These spores are sculptured with elongated elevations or depressions, which include foveolae, lumina, muri and rugulae. Some of these elevations may be coalescent.

Genera :

Uvaesporites Döring (1965) p. 39 pl. 9 figs. 1 - 4 (and pl. 39 fig. 8)

Botanical affinities:

Group : Lycopodialean (possibly Filicalean) (Couper 1958)

Foveosporites Balme (1956) p. 17 pl. 1 fig. 15

Botanical affinities:

Group : Lycopodialean

Family : Lycopodiaceae (Balme 1957, Filatoff 1975)

Lycopodiumsporites Thiegart (1949) emend. Delcourt & Sprumount (1955)

p 31 illustration: Guy (1971) pl. 2 figs. 6 - 14 (and pl. 39 fig. 5)

Botanical affinities:

Group : Lycopodialean

Family : Lycopodiaceae (Dettman 1963)

Lycopodiacidites Couper (1953) emend. Potonié (1956) illustration:

Dettman (1963) pl. 6 figs. 1 - 3 (and pl. 40 figs. 9 - 11)

Botanical affinities:

Group : Lycopodialean

Family : Lycopodiaceae (Dettman 1963)

Varirugosisporites Döring (1965) p. 40 illustration : Couper(1958)

pl. 23 fig. 4

Botanical affinities:

Group : Filicalean

Family : Schizaeaceae (Filatoff 1975)

Ischyosporites Balme (1957) p. 17 pl. 3 fig. 45 (and pl. 40 figs. 4 - 7)

Botanical affinities:

Group : Filicalean

Family : Schizaceae (Couper 1958)

Subturma : Zonotriletes

The Infraturma categories comprising this subturma are delineated on the basis of the position and character of the equatorial thickenings rather than sculpture of the exine.

Infraturma : Tricrassati

Genera :

Staplinisporites Pocock (1962) p 49 illustration : Balme (1957) pl. 5 fig. 62 (and pl. 39 figs. 2 and 3)

Botanical affinities:

Group : Lycopodialean (Filatoff 1975)

Infraturma : Cingulati

Genera :

Densoisporites Weyland & Krieger (1953) p. 12 pl. 4 figs. 13 and 14

Botanical affinities:

Group : Lycopodialean

Family : Sellaginellaceae (Balme 1963)

Neveisporites De Jersey & Paten (1964) p. 8 pl. 5 figs. 11 and 12 (and pl. 39 fig. 9)

Botanical affinities:

Group : Pteridophytic (Filatoff 1975)

Anteturma : Variegerminates

Turma : Aletes

Subturma : Azonoaletes

Genus :

Inaperturopollenites Pflug & Thomson in Thomson & Pflug (1962) p. 64 illustration : Potonie & Venitz (1934) pl. 2 fig. 21 (and pl. 42 figs. 10 - 12)

Botanical affinities:

Group : Coniferales

Family : Cupressae/Taxaceae/Taxiodaceae (Filatoff 1975)

Turma : Saccities

Subturma : Monosaccites

Pollen grains included within this Subturma have one saccus.

Genus :

Callialasporites Sukh Dev (1961) p. 48 illustration : Guy (1971) pl. 4 figs. 15 - 18 (and pl. 42 figs. 3 - 6)

Botanical affinities:

Group : Coniferales

Family : Araucariaceae (Filatoff 1975)

Subturma : Disaccites

Includes bisaccite genera. For a discussion of the dimensional terminology used in the diagnosis of species and genera within this group see Pocock (1962) and Dettman (1963).

Genera :

Vitreisporites Leschik (1956) p. 53 pl. 8 fig. 10

Botanical affinities:

Group : Caytonales (Harris 1961 4, Couper 1958, Filatoff 1975).

Alisporites Daugherty (1941) p. 98 pl. 34 fig. 2 (and pl. 41 figs. 8 - 10)

Botanical affinities:

Group : Pteridosperm (Harris 1961 4, Filatoff 1975)

Pityosporites Seward (1914) pl. 8 fig. 45 (and pl. 41 fig. 7)

Botanical affinities:

Group : Coniferales

Family : Podocarpaceae/Pinaceae (Harris 1961)

Podocarpidites Cookson (1947) pl. 13 fig. 6

Botanical affinities:

Group : Coniferales

Family : Podocarpaceae (Filatoff 1975)

Subturma : Polysaccites

Includes genera with multiple small sacci.

Genus :

Cerebropollenites Nilsson (1958) p. 72 illustration : Couper (1958) pl. 30 fig. 8 (and pl. 41 figs. 4 - 6)

Botanical affinities:

Group : Coniferales

Family : Pinaceae (Couper 1958, Harris 1961)

Turma : Plicates

Subturma : Monocolpates

Genus :

Cycadopites Woodhouse (1933) p. 487 illustration : Wilson & Webster (1946) p. 247 pl. 1 fig. 7

Botanical affinities:

Group : Cycadopsida

Family : Cycadales (Woodehouse 1933)

Turma : Poroses

Subturma : Monoporines

Genera :

Perinopollenites Couper (1958) p. 152 pl. 27 fig. 9 (and pl. 41 figs. 1 - 3)

Botanical affinities:

Group : Coniferales

Family : Cupressae/Taxaceae/Taxiodaceae (Filatoff 1975)

Exesipollenites Balme (1957) p. 39 pl. 11 fig. 123 (and pl. 42 figs. 7 - 9)

Botanical affinities:

Group : Coniferales

Family : Cupressae/Taxaceae/Taxiodaceae (Filatoff 1975)

Classopollis Pflug (1953) p. 91 pl. 16 figs. 29 - 31 (and pl. 41 figs. 11 and 12 and pl. 42 figs. 1 and 2)

Botanical affinities:

Group : Coniferales

Family : Chierolepidaceae (extinct) (Filatoff (1975)

DINOFLAGELLATES

Class : Dinophyceae

Sub-class : Dinoferophcidae

Order : Peridiniales

Family : Gonyaulacystaceae

Type Genus :

Gonyaulacysta Deflandre (1964) emend. Sarjeant (1969) illustration : Gocht (1970) pl. 26 figs. 4 - 9 (and pl. 43 figs. 4 - 6)

Family : Microdiniaceae

Genus :

Lithodinia Eisenack (1935) emend. Gocht (1975) illustration : Sarjeant (1974) fig. 43 (and pl. 44 fig. 1)

Family : Canningiaceae

Genus :

Sentusidinium Sarjeant & Stover (1978) illustration : pl. 44 figs. 2 - 7

Family : Ctenodinaceae

Type Genus :

Ctenodinium Deflandre (1938) emend. Sarjeant (1974) illustration : Gocht (1970) pl. 26 figs. 1 - 3 (and pl. 43 figs. 1 - 3)

Family : Pareodiniaceae

Type Genus :

Pareodinia Deflandre (1974b) emend. Wiggins (1975) illustration : Sarjeant (1974) pl. 13 fig. 5 (and pl. 44 figs. 8 and 9)

other Genus :

Caligodinium Drug (1970b) illustration : Filatoff (1975) pl. 29 fig. 10 (and pl. 44 fig. 10)

Family : Adnatosphaeridiaceae

Type Genus :

Adnatosphaeridium Williams & Downie (1966b) illustration : pl. 43 figs. 7 and 8

GLOSSARY OF DESCRIPTIVE TERMS FOR SPORES AND POLLEN GRAINS

(AFTER DETTMAN 1963)

The spore wall (Sporoderm)

Exine: The outer usually resistant layer of the spore wall

Exoexine: The outer sculptured layer of the exine. Where this layer is stratified the terms outer and inner exoexine may be applied to the outer and inner layers respectively.

Thickenings and extensions of the spore wall

Cingulum: A comprehensive thickening of the equatorial exine.

Corona: Extensions of the equatorial exine in the interradial regions (extensions may be composed of fimbriate-like elements).

Saccus: Approximately equatorially situated air sac (exoexine loosened from the intexine (the inner, non-sculptured layer of the exine).

Terms used in the description of sculpture

I. Minutely sculptured (after Couper 1958 p. 102)

Scabrate: Flecked; with minute pits or elevations less than 1u in size.

II. With cavities or depressions (not less than 1u in size)

Foveolate: With cavities (pits) up to 2u in diameter, or if larger, too widely spaced to form a reticulum.

Foveo-reticulate: with pits large enough and close enough together to form a reticulum, composed of pits (lumina or lacunae) and intervening walls (muri) which separate them.

III. With projections or elevations (not less than 1u in height)

Projections;

Capilli: In which the terminations are branched, the column straight sided or constricted, the height greater than basal diameter.

Clavae: Terminations are constricted, their height greater than basal diameter.

Papillate: Apex rounded to truncate, trunk not markedly tapering, - (setulae of Dettman 1963 i.e. straight sided projections in which the terminations are bluntly tapered).

Elevations:

Bacula: Straight sided flat-topped elevations.

Costate: Ribbed, regular well-defined elevations encircling the spore.

Lophate: Ridged with simple flanged like ridges (usually anastomosing).

Lophate-reticulate: Ridges anastomosing.

Rugulae: Wrinkled, elements irregularly distributed, long and narrow in surface view.

Spina: Elevations in which the height is at least twice the basal diameter, apeces pointed.

Spinulae: As above, where the height is less than twice the basal diameter.

Verrucae: Bases are approximately isodiametric and greater than 1u in diameter.

Granula: Approximately isodiametric elevations up to 1u in diameter.

GLOSSARY OF THE TERMINOLOGY USED IN THE CLASSIFICATION AND DESCRIPTION OF THE DINOFLAGELLATES (AFTER SARJEANT 1974)

General Morphology

Peridinales: The armoured dinoflagellates which possess a rigid theca (wall).

Tabulation: The arrangement of plates comprising the theca (which is extremely constant for any particular species and is, at present, the foundation of their classification.

Apex: The most anterior pole.

Antapex: The opposite pole to the apex.

Horns: Antapical, apical or lateral extensions of the theca.

Crests or Septa: Flanges, which may be spinose or smooth at their distal margins.

Major Cyst Groups

Proximate: Two wall layers in general contact, separating only when horns are developed at the apex or antapex. Usually indented at a position corresponding to the cingulum, the transverse groove which accommodates the transverse flagellum. Tabulation may be reflected in part, or in detail, by crests corresponding to the sutures e.g. Gonyaulacysta, or not at all e.g. Pareodinia. Surface may be ornamented by short spinelets, but without large processes.

Ornamentation

Verrucate: Irregular, wart-like

Spinose: Very short spines

Laevigate: Smooth

APPENDIX 1

PART III

A - Similarity matrix for SMT1A excluding individuals 12 - 15 i.e. Callovian steneosaurs only.

standardised data, including:

Ai - Entire similarity matrix

B - Nearest neighbour scores for SMT1A, standardised data, including:

Bi - Units 1 - 9

Bii - Units 10 - 17

C - Nearest neighbour scores for SMT1A excluding individuals 12 - 15, standardised data, including:

Ci - Units 1 - 11, 16 and 17

D - Similarity matrix for the complete Metriorhynchus sample - SMT, including:

Di - Similarity coefficients for individuals 1 - 10.

Dii - Similarity coefficients for individuals 11 - 20

Diii - Similarity coefficients for individuals 21 - 49

E - Similarity matrix for SMT "adults" only; i.e. the restricted Metriorhynchus sample, including:

Ei - Similarity coefficients for the following specimens:

4, 5, 6, 7, 8, 9, 10, 12, 17, 18.

Eii - Similarity coefficients for specimens 19 and upwards excluding 24, 34, 40, 48 (see p. 49 and figs. 25, 26 and 32).

F - Nearest neighbour scores for SMT, i.e. Metriorhynchus including:

Fi - Units 1 - 24

Fii - Units 25 - 49

13 NO OF VARIATES 9

ES:

3 3 3 3 3 3 3

AMETERS:

3. 3. 3. 3. 3. 3. 3. 3.

144 51 37 57 230 101 160

(Ai)

IG OBSERVATIONS 12

1	2	3	4	5	6	7	8	9	10	11	16	17
1000												
807	1000											
779	868	1000										
599	747	773	1000									
132	325	276	499	1000								
361	554	477	694	770	1000							
414	565	481	714	757	880	1000						
553	704	674	833	570	765	799	1000					
263	477	476	681	796	883	817	770	1000				
294	463	401	611	808	834	845	677	873	1000			
756	771	792	592	233	412	434	573	430	404			
673	762	777	842	475	670	663	810	617	565			
874	815	816	580	148	343	385	578	318	279			
										1000		
										594	1000	
										823	644	1000

(Bi)

	NEIGHBOURS	SCORES
UNIT 1		
	17	876
	2	804
	3	774
	11	756
	16	674
UNIT 2		
	3	869
	17	810
	1	804
	11	771
	16	758
UNIT 3		
	2	869
	17	812
	11	791
	4	778
	1	774
UNIT 4		
	14	857
	15	847
	16	841
	8	835
	12	817
UNIT 5		
	13	832
	10	807
	9	794
	12	779
	6	771
UNIT 6		
	7	884
	9	882
	13	854
	10	832
	14	779
UNIT 7		
	6	884
	10	842
	14	831
	13	831
	9	819
UNIT 8		
	14	886
	4	835
	15	827
	16	810
	7	799
UNIT 9		
	12	903
	13	882
	6	882
	10	874
	7	819

(Bii)

PS1,1 T1 77/08/02 15.22.38 15.28.05 0:03:150 VAMP/3 MK

UNIT 10

13 937
12 901
9 874
7 842
6 832

UNIT 11

17 821
3 791
2 771
1 756
15 636

UNIT 12

9 903
10 901
13 879
15 845
4 817

UNIT 13

10 937
9 882
12 879
6 854
5 832

UNIT 14

8 886
15 864
4 857
7 831
16 800

UNIT 15

14 864
4 847
12 845
8 827
7 807

UNIT 16

4 841
8 810
14 800
3 773
2 758

UNIT 17

1 876
11 821
3 812
2 810
16 645

BATHONIAN. STENEOSAURS

****

	NEIGHBOURS	SCORES
UNIT 1		
	~~13~~ 17	874
	2	807
	3	779
	11	756
UNIT 2		
	3	868
	~~13~~ 17	815
	1	807
	11	771
UNIT 3		
	2	868
	~~13~~ 17	816
	11	792
	1	779
UNIT 4		
	~~12~~ 16	842
	8	833
	3	773
	2	747
UNIT 5		
	10	808
	9	796
	6	770
	7	757
UNIT 6		
	9	883
	7	880
	10	834
	5	770
UNIT 7		
	6	880
	10	845
	9	817
	8	799
UNIT 8		
	4	833
	~~12~~ 16	810
	7	799
	9	770
UNIT 9		
	6	883
	10	873
	7	817
	5	796
UNIT 10		
	9	873
	7	845
	6	834
	5	808
UNIT 11		
	~~13~~ 17	823
	3	792
	2	771
	1	756
UNIT ~~12~~ 16		
	4	842
	8	810
	3	777
	2	762
UNIT ~~13~~ 17		
	1	874
	11	823
	3	816
	2	815

****

(Ci)
Nearest neighbours

SMTIA exc 12-15

Vars 2-10
Var 1.

i.e. Callovian steneosaurs only

(Ci)

(D1)

1000									
902	1000								
948	880	1000							
854	743	823	1000						
795	663	796	911	1000					
738	611	751	887	875	1000				
762	634	769	881	898	910	1000			
764	636	765	917	882	956	909	1000		
793	676	783	916	839	885	838	870	1000	
788	672	858	923	902	936	897	930	889	1000
853	768	905	779	758	743	780	740	741	818
738	655	794	938	935	936	870	926	882	942
824	742	837	860	833	812	877	803	782	865
836	753	863	855	825	809	866	799	799	855
912	829	939	826	794	764	805	766	773	817
833	952	857	700	644	670	651	679	680	744
798	643	791	940	950	897	959	899	907	928
723	625	729	883	908	918	926	925	829	900
915	838	917	896	876	786	835	822	816	867
763	639	788	894	843	948	920	966	863	933
752	674	764	909	887	918	899	925	864	910
717	616	727	882	875	950	897	943	840	898
782	691	805	912	946	890	906	880	836	923
775	885	795	637	594	651	681	642	622	716
782	669	804	912	908	931	931	944	831	933
824	681	797	906	907	865	916	879	860	889
27384	296	422	577	626	635	623	616	522	608
28721	571	740	792	859	778	843	769	708	816
29528	367	515	655	714	762	775	772	630	705
30494	369	472	627	677	732	741	729	612	679
31326	220	338	494	543	566	564	532	454	508
32548	434	511	619	708	659	722	646	595	714
33483	354	506	600	685	603	662	578	538	650
34795	728	803	754	749	700	720	710	673	754
35585	374	503	681	741	730	778	730	676	748
836	725	817	941	885	853	883	889	860	874
828	717	828	972	889	905	928	933	903	940
815	696	822	891	913	872	933	866	853	876
828	669	814	964	908	918	941	932	928	959
823	711	820	876	929	859	876	843	815	896
872	698	862	960	877	924	931	950	938	938

669	521	660	816	849	918	907	905	805	835
828	727	846	956	922	891	925	917	880	943
713	596	722	853	922	901	878	899	787	835
803	687	811	920	875	908	947	924	880	936
770	725	767	913	871	844	844	882	848	860
820	722	832	937	892	919	884	920	937	954
808	840	833	668	647	633	669	629	630	731
754	644	739	901	879	861	871	873	862	842

	11	12	13	14	15	16	17	18	19	20
	1000									
	752	1000			1000					
	911	786	1000		830	1000				
	933	785	979	1000	807	619	1000			
	919	760	912	918	758	593	904	1000		
(Dij)	798	697	757	765	922	805	882	815	1000	
	793	869	888	881	801	711	903	910	819	1000
	717	922	808	795	781	651	882	936	856	908
	862	853	879	901	796	652	883	909	799	922
	775	882	843	832	851	662	952	942	865	865
	740	951	818	804	810	924	598	566	740	701
	716	927	839	827	828	705	934	941	864	933
	771	935	879	862	821	612	928	885	891	887
	850	605	809	790	451	190	537	656	508	609
	771	932	861	839	765	522	880	853	777	760
	817	874	933	904	538	323	772	807	590	750
	457	642	510	496	518	276	699	766	560	712
28	798	836	842	833	362	248	461	569	435	554
	573	733	624	613	605	293	756	719	572	633
	543	731	615	592	548	275	665	671	562	563
(31)	418	530	412	391	824	639	759	681	745	711
	581	646	685	682	507	357	738	827	620	729
	575	599	605	596	824	717	931	882	900	871
34	833	707	821	807	812	719	948	901	885	930
	529	729	629	555	860	655	957	868	849	873
	762	917	845	835	828	643	953	884	899	919
	773	918	848	837	853	658	902	856	852	839
	819	832	879	887	875	677	943	853	896	957
	842	944	946	895	683	573	861	895	742	892
	795	853	889	881	840	722	977	893	910	918
	856	903	954	924	708	604	873	933	795	852
	712	884	757	746	854	709	934	889	861	933
	793	902	883	873	787	582	866	919	857	846
	671	910	751	738	842	715	909	883	855	903
	816	887	899	897	827	837	677	606	751	665
	734	920	806	794	743	596	922	924	822	852
	788	914	832	842						
	885	636	795	817						
	683	934	776	754						

	1000									
	920	1000								
	940	897	1000							
Diii	607	644	635	1000						
	953	956	932	677	1000					
	886	875	933	590	948	1000				
	640	684	598	211	598	518	1000			
	793	790	885	574	817	880	641	1000		
	769	745	677	375	678	734	752	775	1000	
	745	718	650	307	650	676	835	744	929	1000
	553	612	585	269	586	443	775	620	685	745
	568	651	703	346	635	736	721	816	854	847
	620	628	680	328	611	634	778	795	825	836
	684	712	788	692	783	781	413	812	600	566
	768	728	795	335	739	746	714	879	922	883
	921	866	887	652	917	917	575	771	658	627
	909	875	898	661	927	916	552	775	712	674
	841	849	903	666	875	902	551	854	711	663
	934	909	917	622	936	960	489	850	682	632
	832	871	975	629	931	916	517	902	673	629
	912	913	877	655	934	932	398	794	624	547
	899	924	847	594	883	825	695	825	840	816
	903	878	926	664	941	937	544	808	701	663
	911	911	887	541	901	887	674	813	747	723
	901	903	894	712	925	901	570	801	738	690
	906	837	893	524	853	856	625	815	746	727
	909	895	916	671	913	857	563	776	706	671
	629	605	680	890	680	701	347	705	490	460
	909	859	898	538	874	917	599	808	703	673
	1000									
	674	1000								
	738	956	1000							
	381	679	671	1000						
	825	830	811	692	1000					
	502	590	567	729	704	1000				
	473	652	578	717	731	945	1000			
	464	733	679	788	730	845	895	1000		
	507	661	618	871	714	942	979	918	1000	
	430	733	680	795	750	864	855	888	921	1000
	505	540	498	943	680	938	980	942	966	909
	628	715	683	671	806	809	840	836	879	787
	464	681	606	740	745	938	962	926	990	887
	637	686	663	709	770	853	858	827	854	893
	483	684	616	749	670	904	954	917	957	867
	538	691	668	702	847	890	897	843	866	816
	476	661	617	742	691	876	930	906	926	849
	335	524	518	863	448	651	662	726	750	684
	557	639	616	679	846	922	909	833	899	884
	1000									
	870	1000								
	969	832	1000							
	819	906	872	1000						
	981	855	937	826	1000					
	833	829	889	848	851	1000				
	956	848	916	837	930	887	1000			
	776	601	682	581	705	626	686	1000		
****	868	831	895	875	855	905	846	572	1000	

PS1,1 T1 78/09/04 15,31,34 15,32,26 0:00:645 VAMP/3 MK 3.0 PAGE 1

NO OF UNITS 36 NO OF VARIATES 11
VARIATE TYPES:
3 3 3 3 3 3 3 3 3 3
0
SCALING PARAMETERS:
0. 0. 0. 0. 0. 0. 0. 0. 0. 0.
0.
RANGES:
272 281 184 136 67 170 132 66 143 117
2

NO. OF MISSING OBSERVATIONS 78

(Ei)

1000									
885	1000								
861	835	1000							
862	876	885	1000						
901	845	943	888	1000					
898	801	865	808	843	1000				
913	874	922	874	914	882	1000			
925	917	924	845	909	862	929	1000		
919	933	861	946	869	872	903	857	1000	
852	877	888	906	899	783	871	902	869	1000
864	844	727	798	775	769	835	817	847	766
877	801	931	899	958	838	921	858	873	882
881	845	892	870	901	829	884	936	840	917
856	838	934	869	925	814	876	916	844	877
895	932	863	889	850	811	898	924	938	929
898	886	913	920	930	809	915	921	918	923
872	877	816	885	842	806	852	840	902	846
450	506	505	496	489	372	491	541	379	544
597	664	714	731	730	566	652	695	712	778
531	587	655	679	656	517	608	669	600	707
339	394	414	424	381	283	378	404	277	433
547	657	582	661	570	519	651	576	688	663
519	624	515	586	487	452	572	526	574	606
557	635	622	711	623	548	663	617	631	759
925	857	818	866	866	826	851	902	909	857
966	858	882	917	920	881	930	899	931	876
867	893	833	914	831	819	846	793	944	827
952	878	896	923	916	902	945	929	934	846
944	836	897	908	931	914	917	868	923	795
773	807	894	880	878	763	801	861	815	867
947	899	860	910	898	851	928	878	969	863
812	898	872	857	867	738	793	882	831	918
906	838	879	931	904	858	922	859	911	850
877	826	798	806	845	798	826	897	818	899
920	853	897	854	896	929	945	891	879	843
880	853	830	850	847	819	816	931	896	915

(Eii)

1000									
773	1000								
813	882	1000							
746	897	897	1000						
832	832	926	874	1000					
836	918	942	949	914	1000				
860	848	847	830	916	934	1000			
376	481	526	577	497	494	356	1000		
508	700	728	694	627	623	660	694	1000	
461	644	681	635	582	579	571	796	911	1000
287	414	415	482	498	494	254	709	600	668
485	551	597	580	648	562	665	648	819	801
468	465	541	547	615	529	536	733	790	794
515	647	680	618	741	666	648	614	898	844
876	846	902	837	866	906	888	467	599	552
851	917	883	847	876	915	887	423	660	606
817	839	792	803	884	851	869	400	652	565
872	898	911	885	892	920	947	309	598	509
865	942	874	884	839	914	903	175	518	384
681	863	877	903	820	864	769	591	807	764
884	897	874	846	909	931	916	411	644	590
743	815	887	885	862	876	853	576	717	657
828	915	869	872	869	911	862	424	685	600
814	807	878	790	870	821	808	513	707	666
810	878	878	870	894	895	807	422	649	583
778	824	891	832	888	856	886	490	665	617

1000									
583	1000								
677	946	1000							
752	780	755	1000						
378	513	480	621	1000					
328	582	491	649	930	1000				
289	675	606	618	816	874	1000			
333	567	513	604	926	972	890	1000		
306	410	355	554	919	974	923	950	1000	
503	646	610	728	772	805	786	843	820	1000
316	616	523	667	927	953	912	987	959	793
535	634	601	680	818	822	782	810	753	891
313	611	527	539	890	947	893	937	972	810
403	632	608	790	862	865	794	818	765	787
312	588	534	566	846	912	878	901	941	809
442	584	551	801	902	887	801	868	825	800

Spec no.
31-22 - 31+27

31-43

34-45

34-44

1000					
837	1000				
922	777	1000			
856	807	804	1000		
891	787	914	844	1000	
872	853	825	884	807	1000

****

(Fi)

NEIGHBOURS	SCORES
UNIT 1	
3	948
19	915
15	912
2	902
41	872
4	854
UNIT 2	
16	952
1	902
24	885
3	880
48	840
19	838
UNIT 3	
1	948
15	939
19	917
11	905
2	880
14	863
UNIT 4	
37	972
39	964
41	960
43	956
36	941
17	940
UNIT 5	
17	950
23	946
12	935
40	929
44	922
43	922
UNIT 6	
8	956
22	950
20	948
12	936
10	936
25	931
UNIT 7	
17	959
45	947
39	941
38	933
41	931
25	931
UNIT 8	
20	966
6	956
41	950
25	944

PS1,1 T3 78/08/24 17.34.0

22	943
37	933
UNIT 9	
41	938
47	937
39	928
4	916
17	907
37	903
UNIT 10	
39	959
47	954
43	943
12	942
37	940
41	938
UNIT 11	
14	933
15	919
13	911
3	905
48	885
19	862
UNIT 12	
21	951
39	944
10	942
4	938
6	936
23	935
UNIT 13	
14	979
41	954
39	946
26	933
15	912
11	911
UNIT 14	
13	979
11	933
41	924
15	918
26	904
19	901
UNIT 15	
3	939
19	922
11	919
14	918
13	912
1	912
UNIT 16	
2	952
24	924
3	857

PS1,1 T3 78/08/24 17,34,06 17.

48	837
1	833
15	830
UNIT 17	
43	977
7	959
38	957
39	953
23	952
5	950
UNIT 18	
23	942
25	941
21	936
44	933
7	926
8	925
UNIT 19	
15	922
3	917
1	915
43	910
14	901
36	900
UNIT 20	
8	966
41	957
6	948
45	933
25	933
10	933
UNIT 21	
25	953
12	951
23	940
18	936
39	934
8	925
UNIT 22	
25	956
6	950
8	943
12	927
42	924
20	922
UNIT 23	
40	975
17	952
5	946
18	942
21	940
12	935
UNIT 24	
16	924
48	890

(Fii)

UNIT 25

2	885
11	850
15	810
13	809
22	956
21	953
26	948
8	944
43	941
18	941

UNIT 26

39	960
25	948
43	937
23	933
13	933
41	932

UNIT 27

30	835
33	778
31	775
29	752
32	721
35	714

UNIT 28

40	902
23	885
26	880
17	880
35	879
5	859

UNIT 29

30	929
35	922
32	854
42	840
33	825
18	807

UNIT 30

29	929
35	883
32	847
33	836
27	835
42	816

UNIT 31

35	825
27	775
30	745
33	738
29	685
32	674

UNIT 32

33	956

PS1,1 T3 78/08/24 17.34.06 1

UNIT 33

29	854
30	847
35	830
28	816
17	756
32	956
30	836
29	825
35	811
28	795
27	778

UNIT 34

41	943
39	871
48	863
11	833
15	824
13	821

UNIT 35

29	922
30	883
28	879
46	847
49	846
32	830

UNIT 36

37	945
39	942
4	941
43	938
41	938
17	931

UNIT 37

41	980
39	979
4	972
43	962
45	954
17	948

UNIT 38

17	957
41	942
7	933
43	926
39	918
45	917

UNIT 39

43	990
37	979
41	966
4	964
26	960
10	959

UNIT 40

PS1,1 T3 78/08/24 17.34.06 17.35.05 0:02:605 VAMP/3 MK 3.

UNIT 41

23	975
25	931
5	929
39	921
26	916
41	909
45	981
37	980
43	969
39	966
4	960
20	957

UNIT 42

22	924
6	918
7	907
44	906
8	905
21	899

UNIT 43

39	990
17	977
41	969
37	962
4	956
10	943

UNIT 44

18	933
5	922
22	911
21	911
12	910
42	906

UNIT 45

41	981
39	957
37	954
7	947
43	937
10	936

UNIT 46

12	920
18	919
4	910
21	906
49	905
37	897

UNIT 47

41	956
10	954
9	937
4	937
45	930
37	930

PS1,1 T3 78/08/24 17.34.06

UNIT 48

24	890
11	885
34	863
2	840
16	837
3	833

UNIT 49

12	934
18	924
36	922
17	922
26	917
37	909

****